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THE CLASSIFICATION OF THE FREE-LIVING NEMATODES AND THEIR RELATION TO THE PARASITIC NEMATODES

(With Eight Plates)

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ERRATA

On pages 29 and 30, the portion under the heading "Subfamilies and genera of the family Anguillulidae" should read as follows:

- Subfamily Anguillulinae.
  - Genera: *Rhabditis* Dujardin, 1845 (sg. *Rhabditella* Cobb, 1929); *Rhabditoides* Goodey, 1929; *Asymmetricus* Kreis, 1930 (syn. *Pseudorhabditis* Kreis, 1929, preocc.); *Diploscapter* Cobb, 1913; *Hyalaimus* Cobb, 1920; *Hemicycliophora* de Man, 1921; *Cheilobus* Cobb, 1924; *Anguillula* O. F. Mueller, 1783 (syn. *Turbatrix* Peters, 1927 *); *Macrolaimus* Maupas, 1900; *Myolaimus* Cobb, 1920; *Himatidiophila* Rahm, 1924.
- Subfamily Steinerneminae.
  - Genera: *Neoaplectana* Steiner, 1929; *Steinernema* Travassos, 1927c (syn. *Steineria* Travassos, 1927a, preocc.).
- Subfamily Cephalobinae.
  - Genera: Read as printed in original at top of p. 30.
- Subfamily Cephalobiinae.
  - Genus: *Cephalobium* Cobb, 1920. Delete subsequent reference to Peters, as this refers to *Turbatrix*, as noted above, and not to *Cephalobium*.

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* The objections of Peters to the use of the old name, well established and universally used since Bastian, are at least questionable. Even if they should prove to be valid, an exception to the rules of priority should be made for this case.

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By I. N. FILIPJEV,

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(With Eight Plates)

There are several opinions as to the position of the Nematoda in the animal kingdom. Cobb (1920) suggests that they constitute an independent phylum. There is much in favor of that point of view, as the Nematoda do not have very near relatives among other animal forms. However, in dealing with forms of such low organization as the nematodes, we must consider not only the purely morphological peculiarities, but the general structure and embryology as well. A consideration of these things shows that there are some related forms, perhaps not so very closely related, but with the same chitinous cuticle and bilateral determinative type of cleavage. The group received its definition, as well as its name, from Grobben, who called it Aschelminthes and included in it the Rotatoria, Gastrotricha, Echinoderida, Nematoda, Gordiacea, and Acanthocephala. Besides the above-mentioned embryological resemblance, all of these have the following common features: A functional primary body cavity, absence of a circulatory blood system, an anal opening if there is an intestine, a more or less cylindrical form of body with a circular cross-section, and a firm external cuticula. The recognition of this group is very convenient and as yet is not contrary to our knowledge of these forms, although not all of its members show unquestioned relationships (cf. Brandes).

The last three groups are often treated together as a phylum or class, the Nemathelminthes. This does not seem to be an entirely satisfactory point of view, especially as regards the Acanthocephala, which are compared by Cholodkovsky to the Platodes, although recently Meyer has found that the type of cleavage is the same as in the Rotatoria. The Gordiacea, although showing a greater resemblance, are, of course, not directly connected with the Nematoda (Vejdovsky). Heider's discussion also seems to permit of recognizing a systematic relationship among these groups.

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Probably the most convenient systematic arrangement would be one which treated the Aschelminthes as a phylum or subphylum, if one is inclined to retain the useful group Vermes as a phylum. The Nematoda would then be a class. But if one considers the Nematoda as a phylum, it seems impossible as yet to distinguish classes within the group. In the animal kingdom a class is a unit of very high morphologic differentiation. Such differences do not seem to exist among the various groups of Nematoda, their organization being very uniform when compared with the classes of a well-established phylum, such as the Mollusca or Vertebrata. If it is a phylum, it is a phylum with only one class.

The class Nematoda could be defined as having, in addition to the chief characters shared with the other Aschelminthes, the following characters:

Small worms, consisting of comparatively few cells; body elongated, bilateral in structure, although without a physiological differentiation between dorsal and ventral sides; with a hard external cuticula; with a single layer of longitudinal muscle cells, divided by two large lateral epidermal thickenings, the lateral cords; a muscular esophagus, usually with a triangular lumen; separate sexes; double genital organs, the female genital opening being situated in the ventral line, as a rule, at varying points from anterior to posterior; in the male the terminal genital tract and the posterior intestine unite and have a common aperture; with a very feeble regenerating power and an absence of cilia.

There are several exceptions to this definition, but they are manifestly secondary. The purpose here is neither to discuss these exceptions nor to advance theories as to how they arose. The feature which should be expressly pointed out is the importance of the cuticula in the nematode history. It could be considered as differentiating the Nematoda as a separate group, because their simple musculature, and, in this connection, the peculiar mode of motion, the absence of power of regeneration, and the peculiar biology of many of them, are possible only by virtue of the presence of this cuticular armor.

The classification of the Nematoda is in a rather bad state. Much has been gained in the last 15 years in arranging the parasitic forms, and several systems have been proposed for the free-living ones. But inasmuch as the systems for the two groups are widely different, an attempt to combine the two in one whole was made only by Baylis and Daubney, but it must be regarded as wholly inadequate where it deals with the free-living forms.

The first question arising in any attempt at nemic taxonomy is the general relation of the free-living and parasitic forms. Until recently there have been expressed in the literature opinions to the effect that the Nematoda are chiefly parasitic, a small part of them being free-living, mostly living in decaying substances. That point of view is completely wrong and is, of course, merely a result of the historical sequence in the study of this group, because in its early development much more attention was paid to the larger and economically more important parasites than to the inconspicuous and apparently economically unimportant free-living forms.

The comparison of the number of described species in both groups is somewhat suggestive. The very approximate number of species described up to the end of 1930 is as follows:

Order	Free-living		Parasitic in—		Total
	Marine	Fresh-water and soil	Invertebrates	Vertebrates	
Enoplata	450	380	110	——	940
Chromadorata	350	110	——	——	460
Desmoscolecata	60	——	——	——	60
Monhysterata	310	60	——	——	370
Anguillulata	5	440	30	610	1,085
Oxyurata	——	——	90	320	410
Ascaridata	——	——	——	240	240
Spirurata	——	——	1	605	606
Filariata	——	——	——	245	245
Dioctophymata	——	——	——	25	25
Trichurata	——	——	——	160	160
	1,175	990	231	2,205	4,601

Free-living, 2,165; parasitic, 2,436.

These figures must be regarded as subject to considerable correction, as it is probable that a much larger number of parasites than of free-living forms are known to science. Systematic studies of the former were begun more than a century ago by Rudolphi in 1819, and since then hundreds of workers have been engaged in a study of them. The study of free-living forms began with Bastian in 1865, almost 50 years later; and it is only in the last 15 years that there has been a notable increase in number of workers, making a total today of about 15 workers engaged in the study of them, which is, of course, a decided gain when compared with two or three working along this line at any one time before about 1912.

In the collections of the parasitic species today there are no more than 20 to 30 percent of new species. In the collections of free-living forms from the fresh waters of Europe, this percentage is even lower, but among the terricolous forms, Cobb (1917) described as new 45 percent of his species of *Mononchus,* and Thorne (1925) described as new 75 percent of his species of *Acrobeles.* This last figure is especially interesting as these are the results of careful collecting in a very restricted area. Among the marine nematodes in each large collection the new species are more numerous than the described ones. Thus from the Black Sea the writer found 80 percent of the species new; from the Glacial Sea, in only one of the best known orders, 70 percent. Steiner (1927) in the *Epsilonematinae* found nearly 100 new species to add to the three which were all those previously known.

Furthermore, the parasitic species are known more or less over the entire world. The free-living nonmarine forms have been most fully studied in Europe, much less in North America and Australia, and very little in the tropical countries. The marine forms also have been systematically studied only in Europe, practically speaking.

From the foregoing it seems probable that the free-living marine species exceed in number, perhaps equal several times the number of, both parasitic and fresh-water species, the two latter being nearly equal in number of species. A comparison of the number of genera would not give an adequate conception because of the lack of uniformity in the classifications of different workers. The parasitic forms seem to be split up more than the free-living ones (cf. Baylis, 1924).

A second line of evidence as to the relations of free-living and parasitic nematodes is in regard to their physiology. The marine forms, probably with secondary exceptions among the few marine Anguillulidae, are in free relations with the external world, the water enters into their body through the cuticula, and probably the ion concentration is the same outside the body as inside. If one puts a marine nematode in a solution of some intravitam stain, for instance, methylene blue, the first things to be colored are the granulations of the skin and the peripheral nerve endings included therein. Then the stain is concentrated in phagocytic cells, some muscles, deeper-lying nerve cells, etc. In fresh-water forms the color penetrates through the cuticula more slowly, and penetrates chiefly through the thin cuticula of the papillae, and through the mouth, anal, and vaginal openings. In the intestinal parasites or in the saprozoic forms, the stain penetrates only through these openings, being chiefly ingested through the mouth, the cuticula being quite impermeable to the stain. We know that the internal fluids of the latter forms are of peculiar chemical and osmotic composition, quite different from their external medium which is sometimes variable. The relations existing in marine nematodes, as well as in other marine animals, are generally regarded as primary ones, and we have no reason to consider them as secondary in the nematodes in general.

There are several morphological structures leading us to the same conclusions, as, for example, the cervical gland or renette. In free marine forms this appears mostly as a simple skin gland, participating in the general mosaic of the body epithelium just as do the ordinary epithelial cells. It is more complexly developed in parasites or saprozoic forms, having in its primary form two outgrowths lying before and two behind the cervical pore. In young *Ascaris* larvae it is a rounded cell only, the outgrowths appearing in its later development. But throughout the parasitic nematodes it is always the same unicellular skin gland as it is in the free-living forms, as was shown 30 years ago by Jägerskiöld and Golovin. It probably has a function similar to that of the protonephridia, to which it was compared by Cobb (1890–1891), Steiner (1920), and some others, in that the latter organs also are skin glands of one sort. The nematode excretory apparatus is more primitive than the nephridia. The structure of a comparatively complexly developed organ consisting of only one cell (or sometimes of two, which makes no difference in principle) could be considered only as a secondary matter. Its excessive and complex development in saprozoic and parasitic forms is probably correlated with the necessity for an independent osmotic relation to the external medium.

Another point of comparison is the cell constancy of the parasites, affecting in some instances all their organs except the genitalia (cf. Martini, 1916). In musculature it is known as meromyarity and, since A. Schneider, has been regarded by many scientists as a very important systematic character. I do not consider this character as a primary one; really it means that there are less cells, but that each cell is more complex. The primitive condition is, of course, an indeterminate number of cells not highly differentiated. Therefore we could not regard these forms as primitive ones, but merely as neotenic larvae of forms with determinate development. The large parasitic forms could be considered as hypertrophic larvae (cf. Filipjev, 1918, 1927). The full-cell nematodes are found mostly among marine forms.

All this speaks in my opinion for the primitiveness of free-living nematodes and especially the marine ones.

But we hardly could point to these differences for a primary division into two orders or subclasses as was proposed by Perrier and apparently on ground of convenience by Stiles and Hassall (1926). Bastian's classical words that the organization of free-living forms "as a whole, differs in no obvious or important manner from that of their parasitic kindred" hold true today. Moreover, the differences between systematic groups within the broad groups of parasites and free-living nematodes, and an apparent absence of intermediate forms between them, demands a direct division of Nematoda into several orders without any subclasses. If one wishes to use such a division, then the dividing line must be drawn between the Anguillulata and the other free-living forms, rather than between the Anguillulata and the parasitic ones.[1]

A proposed classification is presented herewith:

Class NEMATODA
- Order ENOPLATA
  - Family Enoplidae
  - Trilobidae
  - Dorylaimidae
  - Mermitidae
- Order CHROMADORATA
  - Family Camacolaimidae
  - Plectidae
  - Chromadoridae
- Order DESMOSCOLECATA
- Order MONHYSTERATA
  - Family Monhysteridae
  - Linhomoeidae
- Order ANGUILLULATA
  - Family Anguillulidae
  - Tylenchidae
  - Strongylidae
- Order OXYURATA
- Order ASCARIDATA
- Order SPIRURATA
- Order FILARIATA
- Order DIOCTOPHYMATA
- Order TRICHURATA

KEY TO ORDERS OF NEMATODA

1\. (8) Tail with tail glands and spinneret (when without, then with amphids pocketlike). Amphids of various forms, mostly well developed. Mostly free-living, nonsaprozoic.

2\. (3) Amphids pocketlike. Cuticle smooth. Bulb absent. Ovaria reflexed. Free-living, marine or fresh-water and soil-inhabiting, or parasites of insects .... **Enoplata**

3\. (2) Amphids spiral or of derived form; circular, bubble-like, horseshoe-shaped, or transverse and slitlike.

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[1] All parasitic forms studied by Martini (1906, 1909) have a primary division of the epidermis into six cell rows, but the few Enoplata studied by Retzius and by Filipjev (1912, 1923) have eight. The scarcity of forms studied does not as yet permit one to draw any decisive conclusions.

Cuticle annulated or smooth. Bulb present or absent.

4. (7) Cuticle annulated or smooth, without secreted rings or setaceous appendages; or if setaceous, then with ordinary spiral amphids.

5. (6) Ovaries reflexed. Cuticle annulated. Free-living marine, fresh-water or soil forms .... **Chromadorata**

6. (5) Ovaries straight. Cuticle annulated or smooth. Free-living, mostly marine forms .... **Monhysterata**

7. (4) Cuticle with 12 to 84 coarse secreted annules or setaceous appendages. Amphids bubblelike. Free-living marine forms .... **Desmoscolecta**

8. (1) Tail without tail glands and spinneret. Amphids poorly developed, slit or papillalike, never pocketlike. Saprozoic or parasitic.

9. (12) Esophagus with a cardiac or middle bulb, sometimes degenerated or completely lost. Free-living, saprozoic or parasitic.

10. (11) Body without a large body cavity. Renette not very prominent. Free-living saprozoic or parasites of invertebrates .... **Anguillulata**

11. (10) Body with large body cavity. Renette very prominent, with four large longitudinal ducts. Parasites of the intestines of vertebrates and invertebrates .... **Oxyurata**

12. (9) Esophagus muscular or tubular, always well developed, without a bulb. Parasites of vertebrates.

13. (16) Male with a well-developed bell-shaped bursa.

14. (15) Bursa with longitudinal ribs ...... **Anguillulata** (Strongylidae)

15. (14) Bursa without ribs .... **Dioctophymata**

16. (13) Male without a bursa, or male absent in the parasitic stage.

17. (24) Esophagus normal or with reduced musculature.

18. (19) Head with three well-developed lips. Parasites of intestines .... **Ascaridata**

19. (18) Head with two or four prominent lips or three obscure ones.

20. (23) Parasites of intestines or respiratory system.

21. (22) Head with three poorly developed lips or without lips. Parasitic generation syngonic; digenetic, free-living bisexual generation rhabditoid ..... **Anguillulata** (Rhabdiasinae)

22. (21) Head with two or four lips .... **Spirurata**

23. (20) Parasites of tissues or circulatory system of vertebrates. Head with two lips or without lips. Esophagus often without musculature .... **Filariata**

24. (17) Esophagus tubular, consisting of one row of cells. Body very narrow, filiform in its anterior part .... **Trichurata**

Order ENOPLATA

The Enoplata were defined by Filipjev (1918, 1927) primarily as a family, and this was directly divided into several subfamilies.

All these have a smooth cuticle, except for only a very few forms which have a very fine striation. The esophagus is uniform, without a bulb (fig. 1). The head presents a typical structure, bearing the typical six labial papillae, ten cephalic setae, in some forms transformed into papillae, and two amphids (figs. 4, 5), the latter present in the form of a pocket, with an anterior aperture (figs. 2, 3, 4); the cuticle on the head presents a very typical reduplication with a circular cavity around it, bordered behind by the so-called cephalic line (figs. 2, 4); the esophagus adjoins the inner layer of the cephalic cuticle along a very wide surface (figs. 2, 3). The ovaries are always reflexed (fig. 1). The musculature is polymyarian. Some of these nematodes are the largest of all free-living nematodes. There are exceptions to nearly all these characters inside the order, but most of these are present in any given form discussed here.

KEY TO FAMILIES OF ENOPLATA

1\. (2) Cuticle with duplication on the head. Males mostly with one or two preanal tubes. Most genera marine .... **Enoplidae**

2\. (1) Cuticle without duplication on the head.

3\. (6) Esophagus with muscles. Free-living forms.

4\. (5) Esophagus strong, of nearly uniform thickness throughout its whole length. Free-living, fresh-water and marine forms .... **Trilobidae**

5\. (4) Esophagus dorylaimoid, i.e., bottle-shaped, weak, almost without musculature anteriorly, then suddenly enlarged and strongly muscular posteriorly. Free-living, mostly fresh-water and soil forms, some marine forms .... **Dorylaimidae**

6\. (3) Esophagus without muscles, forming a long narrow chitinous tube with some adhering, large, epidermal cells. Adults mostly free-living, soil and fresh-water forms; larvae parasitic in insects and other invertebrates .... **Mermitidae**

Subfamilies and Genera of the Family Enoplidae

Subfamily Leptosomatinae.

Genera: *Anticoma* Bastian, 1865 (syn. *Stenolaimus* Marion, 1870); *Leptosomella* Filipjev, 1927; *Barbonema* Filipjev, 1927; *Platycoma* Cobb, 1893; *Platycomopsis* Ditlevsen, 1926 (syn. *Dactylonema* Filipjev, 1927); *Synonchus* Cobb, 1893 (sg. *Fiacra* Southern, 1914; sg. *Jägerskiöldia* Filipjev, 1916); *Cylicolaimus* de Man, 1889; *Nudolaimus* Allgén, 1929; *Leptosomatum* Bastian, 1865; *Leptosomatides* Filipjev, 1918; *Deontostoma* Filipjev, 1916; *Thoracostoma* Marion, 1870 (sg. *Pseudocella* Filipjev, 1927); *Triodontolaimus* de Man, 1893.

Subfamily Enoplinae.

Genera: *Enoplus* Dujardin, 1845 (syn. *Enoplostoma* Marion, 1870); *Enoploides* Saveljev, 1912; *Filipjevia* Kreis, 1928; *Enoplolaimus* de Man, 1893 (sg. *Mesacanthion* Filipjev, 1927; sg. *Oxyonchus* Filipjev, 1927); *Saveljevia* Filipjev, 1927; *Parenoplus* Filipjev, 1927.

Subfamily Oxystominae.

Genera: *Thalassoalaimus* de Man, 1893; *Nuadella* Allgén, 1927; *Trefusia* de Man, 1893; *Acoma* Steiner, 1916; *Paroxystomina* Micoletzky, 1924; *? Asymmetrica* Kreis, 1929; *Nemanema* Cobb, 1920; *Nemanemella* Filipjev, 1927; *Oxystomina* Filipjev, 1918 (syn. *Oxystoma* Bütschli, 1874, preocc.; syn. *Schistodera* Cobb, 1920); *Halalaimus* de Man, 1888; *Tycnodora* Cobb, 1920; *Nuada* Southern, 1914; *? Xennella* Cobb, 1920.

Subfamily Phanodermatinae.

Genera: *Crenopharynx*, nom. nov. (syn. *Stenolaimus* Southern, 1914, nec Marion, 1870, type *Anoplostoma gracile* Linstow, 1900); *Nasinema* Filipjev, 1927; *Micoletzkyia* Ditlevsen, 1926; *Phanodermopsis* Ditlevsen, 1926 (syn. *Galeonema* Filipjev, 1927); *Phanoderma* Bastian, 1865 (syn. *Heterocephalus* Marion, 1870; syn. *Cophonchus* Cobb, 1920); *Phanodermella* Kreis, 1928; *Klugea* Filipjev, 1927 (syn. *Gullmarnia* Allgén, 1929).

Subfamily Thoracostomopsinae.

Genus: *Thoracostomopsis* Ditlevsen, 1919.

Subfamily Oncholaiminae.

Genera: *Anoncholaimus* Cobb, 1920; *Pelagonema* Cobb, 1893; *Vasculonema* Kreis, 1928; *Pandolaimus* Allgén, 1929; *Pontonema* Leidy, 1855 (syn. *Paroncholaimus* Filipjev, 1916); *Viscosia* de Man, 1890 (syn. *Steineria* Ditlevsen, 1926, preocc.); *Oncholaimus* Dujardin, 1845; *Convexolaimus* Kreis, 1928; *Krampia* Ditlevsen, 1922; *Prooncholaimus* Micoletzky, 1924; *Adoncholaimus* Filipjev, 1918; *Metoncholaimus* Filipjev, 1918; *Filoncholaimus* Filipjev, 1927; *Mononcholaimus* Kreis, 1924; *Oncholaimellus* de Man, 1893; *Anoplostoma* Bütschli, 1874; *Trilepta* Cobb, 1920.

Subfamily Rhabdodemaniinae.

Genus: *Rhabdodemania* Baylis and Daubney, 1926 (syn. *Demania* Southern, 1914, preocc.).

Subfamily Eurystominae.

Genera: *Ditlevsenella* Filipjev, 1927; *Eurystomina* Filipjev, 1918 (syn. *Eurystoma* Marion, 1870, preocc.; syn. *Marionella* Cobb, 1921); *Bolbella* Cobb, 1920; *Thoonchus* Cobb, 1920; *Ledovitia* Filipjev, 1927.

Subfamily Enchelidiinae.

Genera: *Enchelidium* Ehrenberg, 1836 (syn. *Lasiomitus* Marion, 1870; syn. *Calyptronema* Marion, 1870); *Chaetonema* Filipjev, 1927; *Asymmetrella* Cobb, 1920; *Illium* Cobb, 1920; *Catalaimus* Cobb, 1920; *Dilaimus* Filipjev, 1926; *Polygastrophora* de Man, 1922; *Symplocostoma* Bastian, 1865 (syn. *Amphistenus* Marion, 1870; sg. *Isonemella* Cobb, 1920); *Fenestrolaimus* Filipjev, 1927; *Rhinoplostoma* Allgén, 1929; *Pseudodilaimus* Kreis, 1928.

KEY TO SUBFAMILIES OF ENOPLIDAE

1. (10) Buccal capsule surrounded by the esophageal musculature; absent in certain genera.
2. (3) The cephalic armor (i.e., the chitinized part of the external cephalic cuticle) present. Three well-developed lips present. The buccal organs complicated, consisting of three unequally developed jaws (reduced in *Saveljevia*) with a cuticular ring around them, homologous to the cephalic capsule of other forms; onchi in some genera .... **Enoplinae**
3. (2) The cephalic armor absent (in *Phanoderma* there is present, besides the true cephalic capsule, which is always absent in *Enoplinae*, a longitudinally striated cervical armor). Lips mostly absent.
4. (5) Esophageal contour straight; the cephalic circle always single, composed of 10 setae or papillae .... **Leptosomatinae**
5. (4) Esophageal contour crenated.
6. (9) Spear absent; buccal capsule absent or very small.
7. (8) Esophagus broadly incised posteriorly. Body mostly elongate, in some species very thin. Spicules short, preanal tube absent .... **Oxystominae**
8. (7) Esophagus rounded posteriorly. Body mostly moderately elongate. Spicules long, preanal tube present in most forms .... **Phanodermatinae**
9. (6) Spear present, long and thin, followed by a modified part of the esophageal tube loosely articulated with it .... **Thoracostomopsinae**
10. (1) The buccal capsule free (as least for a part), generally with strong chitinized walls (except when reduced as in *Enchelidium*).
11. (14) The buccal capsule closed by six mobile lips, its walls strongly chitinized, mostly bearing three immobile onchi.
12. (13) The walls of the capsule without clefts, therefore completely immobile. Spicules very dissimilar; one preanal tube or none .... **Oncholaiminae**
13. (12) The walls of the buccal capsule with clefts, therefore somewhat mobile. Spicules thin, curved; two preanal tubes .... **Eurystominae** (*Ditlevsenella*)
14. (11) Three lips or none, buccal capsule broadly open.
15. (16) Buccal capsule conoid with chitinous folds in the walls, teeth short .... **Rhabdodemaniinae**
16. (15) Buccal capsule cup-shaped with spear-shaped tooth or teeth, or reduced to form a narrow chitinous tube.
17. (18) Spicules curved, preanal tubes two; one tooth ...... **Eurystominae**
18. (17) Spicules elongated, no preanal tubes; one tooth, three teeth, or none .... **Enchelidiinae**

The Leptosomatinae are the simplest forms, showing all the primitive characters of the family preserved; the mouth organs are mostly very simple (fig. 2). The differentiation goes here in two directions. One development is the hardening of the head by the so called cephalic capsule, simple in *Synonchus* and very complex in *Thoracostoma* (fig. 3). The other development is the acquisition of movable mouth structures; a simple small movable tooth is found in *Leptosomatum* and *Synonchus; Fiacra* and *Platycoma* have three teeth situated more anteriorly, quite near the lips; and *Triodontolaimus* has three large jaws in the same position. *Triodontolaimus* presents a connecting link with the following subfamily.

In the Enoplinae are united several closely related genera. *Enoplus* has three jaws more specialized than in *Triodontolaimus* (figs. 4, 5). The esophagus has here an expanded attachment to the cuticle as in the preceding subfamily. The chitinous ring surrounding the jaws probably corresponds to the cephalic capsule; the outer chitinization of the head, the "cephalic armor", corresponds to the inner layer of the reduplicated head cuticle in the Leptosomatinae. Besides the ordinary head armature of ten cephalic setae and the amphids, there are two "cephalic organs", lateral in position (the "lateral lips" of de Man), another organ of sense, probably present in all Leptosomatinae also. The spicules are often very complex, and a typical glandular and sensitive organ, the "preanal tube", is to be seen anteriorly (it is probably also present in all Leptosomatinae, although less developed). *Enoploides* (fig. 6) presents an enormous development of lips probably correlated with its rapacious habits; the jaws are present but profoundly split posteriorly. In *Enoplolaimus* (fig. 7) the jaws are weak, each in the form of two parallel, chitinous rods connected anteriorly and provided with two hooks spreading sideways; between the rods of the jaws there are true onchi which spread inside the mouth capsule (cf. Saveljev, 1912). The amphid is very small and difficult to see, but the cephalic organ is well developed, sometimes spreading outside the contour of the head and probably substituting in its functions for the reduced amphids. An interesting transformation occurs in the labial papillae in most of the genera; they project anteriorly and greatly resemble setae, but they lack the distinct articulation with the cuticle which is characteristic of true setae.

The Oxystominae are characterized by the excessive elongation of the body. The most primitive forms are very similar to the Leptosomatinae, but in others the elongation involves the head organs. In *Oxystomina* (fig. 8) the amphid is very remote from the anterior end and becomes very much elongated, with a large anterior aperture, the reverse of the common condition. The cephalic circle of the setae is divided into two circles, with six setae in the anterior and four in the posterior circle, an evidence of its complex nature. *Halalaimus* (fig. 9) presents a further step in the elongation of the amphids, so that the primitive pocket form could hardly be recognized without the intermediate *Oxystomina.*

The Phanodermatinae in its most simple members, for example, *Crenopharynx,* closely resembles the Leptosomatinae as regards the structure of the head. The differences are in the always elongated spicules and the esophagus of a distinct cellular structure. The type genus *Phanoderma* (fig. 10) is ocellate and has a cephalic capsule like *Thoracostoma* but of a different type, four-lobed instead of six-lobed, and followed by a cephalic armor probably homologous to that of the Enoplinae. Several other genera closely resemble *Phanoderma.*

The Thoracostomopsinae are very distinctive. The cellular esophagus and the four-lobed cephalic capsule resemble those of *Phanoderma,* but there is a peculiar spear followed by a modified part of the esophageal tube, to which the spear is joined by an articulation.

The Oncholaiminae have a spacious mouth capsule, provided in typical representatives with three immobile onchi (fig. 11). Generally they do not have the preanal organ typical for all the three preceding subfamilies, although *Pontonema* has a reduced one, so its absence in other genera could be considered as secondary. The existence of the spacious mouth capsule does not permit the esophageal musculature to adhere to the cuticle directly as in the previous forms. But there is the same duplication of the cuticle on the head as in *Leptosomatum,* and the cuticle of the mouth capsule is folded in that place. Actually the mouth capsule is nothing other than the enlargement of the interior of the esophageal tube lacking the surrounding musculature; the epidermal cells that form the esophagus in that region adhere over a wide area to the cuticle just as do the muscle cells in other forms. *Krampia* should be considered as a reduced *Oncholaimus,* a parallel to the conditions in *Catalaimus* discussed below.

In the Rhabdodemaniinae, *Rhabdodemania* (fig. 12) is a very distinctive genus, the only genus at present in an isolated subfamily erected for it. The large buccal capsule resembles that in the

Oncholaiminae, but the taxonomic relations of these nematodes are not quite certain.

The Eurystominae (fig. 13) are related to the Oncholaiminae but distinct enough to be separated. They do not have lips around the mouth except in *Ditlevsenella*. In typical genera the single onchium is protrusible. Very characteristic is the spicular apparatus (fig. 14) with the thin and strongly curved spicules and two distinctive preanal organs. In the genus *Bolbella* the esophagus is divided posteriorly into eight bulbi, an exceptional structure, not only among the bulbless Enoplata, but also among all other Nematoda; its mouth capsule and the spicular apparatus are quite typical.

The Enchelidiinae are similar to the Eurystominae as regards the mouth capsule with its protrusible onchium (fig. 15). The long spicules suggest a possible relation to the Phanodermatinae. Oddly enough there exists a polybulbous genus, *Polygastrophora,* with all the peculiarities of the subfamily, parallel to *Bolbella* of the Eurystominae. Very interesting is the disappearance of the mouth capsule in the males of certain genera. De Man (1922c) described a form belonging to *Catalaimus,* in which the male lacks the mouth capsule although the female has a typical one. Such males were known long ago under the name of *Enchelidium* (fig. 16). In describing the Black Sea species, I called attention to the strange fact that only the males of this genus were described by the numerous authors studying them, but only De Man's discovery provided an explanation of the problem. In the head, which is always very narrow, there are two cuticular lenses very similar to those of *Symplocostoma;* the esophageal tube anterior to them is very narrow, as if really reduced. The pigment spot is in the vicinity of the lens. The cuticular lens, as one concludes from comparison with some species of *Symplocostoma,* represents nothing other than the bottom plate of the mouth capsule. Two interesting points are to be noted here: first, that of the change of functions; second, an example of an organ so highly rated by systematists, disappearing in the same species, in the same individual even, during its molts.

SUBFAMILIES AND GENERA OF THE FAMILY TRILOBIDAE

Subfamily Trilobinae.

Genera: *Tripyla* Bastian, 1865 (syn. *Promononchus* Micoletzky, 1923; sg. *Trischistoma* Cobb, 1913); *Diplohystera* Cillis, 1917; *Trilobus* Bastian, 1865 (syn. *Paratrilobus* Micoletzky, 1922); *Cryptonchus* Cobb, 1913 (syn. *Ditlevsenia* Micoletzky, 1925); *Gymnolaimus* Cobb, 1913; *Udonchus* Cobb, 1913; *Onchulus* Cobb, 1920; *Prismatolaimus* de Man, 1880.

Subfamily Mononchinae.

Genera: *Mononchulus* Cobb, 1918; *Mononchus* Bastian, 1865 (sg. *Sporonchulus* Cobb, 1917; sg. *Prionchulus* Cobb, 1916; sg. *Mylonchulus* Cobb, 1916; sg. *Anatonchus* Cobb, 1916; sg. *Iotonchus* Cobb, 1916).

Subfamily Tripyloidinae.

Genera: *Tripyloides* de Man, 1886; *Parachromagaster* Allgén, 1929; *Cothonolaimus* Ditlevsen, 1919 (syn. *Macrolaimus* Ditlevsen, 1919, preocc.); *Bathylaimus* Cobb, 1893; *Bathylaimella* Allgén, 1930; *Halanonchus* Cobb, 1920; ? *Rhabdocoma* Cobb, 1920.

KEY TO SUBFAMILIES OF TRILOBIDAE

1. (2) Buccal capsule free, large, thick-walled; soil and fresh-water forms .... **Mononchinae**
2. (1) Buccal capsule absent, or narrow, or if large never thick-walled, and if free then only to a small extent.
3. (4) Amphids typical, pocketlike; spicular apparatus not complex; fresh-water and soil forms .... **Trilobinae**
4. (3) Amphids mostly atypical, either spiral-shaped or rounded (except *Halanonchus*); spicular apparatus of a complex type, with a large gubernaculum exceeding the spicules in length; marine forms ...... **Tripyloidinae**

The preceding family, with only a very few exceptions, is composed of marine forms; on the other hand, the remaining three families contain mostly fresh-water and soil nematodes, with only comparatively few members occurring in the sea. The Trilobidae, while conserving some of the primitive features of the preceding family, have completely lost the primitive wide attachment of the esophagus to the cuticle of the head. In all its members the esophagus is wide, of nearly the same diameter from the anterior end to the cardia; the cardia is well developed, in some genera with typical glandular cells inside; the caudal glands and the spinneret are present in almost all genera. In the type genus, *Trilobus,* (fig. 17) there is a broad mouth capsule with two denticles at its base. *Tripyla* has a very similar mouth capsule with the same denticles, but it can be closed, thus disappearing almost completely; in such a closed position only the straight contours of its walls anterior to the denticle show the presence of firm, differentiated cuticle. In the preserved specimens of that genus the cuticle is often distinctly striated, but this striation is never apparent in living specimens, the cuticle in these being perfectly smooth as in other members of the Enoplata; the causes of this have never been investigated closely, but probably it is due to some internal striation. In most of the genera there are a larger number of preanal organs instead of one or two as in the Enoplidae. In some, such as *Trilobus,* they are highly differentiated; in others they are represented as simple papillae, a condition which could be considered as more primitive than that in the Enoplidae; in the Enoplidae there is only one genus, *Enchelidium,* that has such a row of papillae.

The second subfamily, the Mononchinae (fig. 1), has a very wide buccal capsule with thick walls. The cephalic setae are transformed into papillae, perhaps because of the method of swallowing prey, since the mouth capsule functions only as a sucker, without any masticating function, and setae would hinder the close adherence of the prey to the lips. Very typical features here are the preanal row of numerous papillae, sometimes transformed into chitinous tubes, and a very strong bursal musculature. The caudal glands and the spinneret are present, with very rare exceptions.

The Tripyloidinae is a group of marine genera resembling in their head characters the Trilobinae, with a typical complex spicular apparatus in all of them. Some doubts as to whether they belong in the Enoplata arise from the shape of the amphids, which are not of the typical pocket form, but are spiral or rounded (fig. 18). In the genus *Halanonchus,* the males of which have the same typical spicular apparatus, the amphids are almost of the pocket type (fig. 19), which makes very probable the interpretation of the form of the others as being of the modified pocket type.

Subfamilies and Genera of the Family Dorylaimidae

Subfamily Alaiminae.
    Genera: *Alaimus* de Man, 1880; *Litonema* Cobb, 1920.
Subfamily Ironinae.
    Genera: *Thalassironus* de Man, 1889; *Dolicholaimus* de Man, 1889; *Ironella* Cobb, 1920; *Trissonchulus* Cobb, 1920; *Syringolaimus* de Man, 1889; *Ironus* Bastian, 1865.
Subfamily Tylencholaiminae.
    Genera: *Diphtherophora* de Man, 1880 (syn. *Chaolaimus* Cobb, 1893); *Pharetrolaimus* de Man, 1922c; *?Ecphyadophora* de Man, 1922c; *Tylencholaimus* de Man, 1876 (syn. *Brachynema* Cobb, 1893, preocc.); *Tylolaimophorus* de Man, 1880, probably synonymous with *Tylencholaimus* (syn. *Archionchus* Cobb, 1913); *Tylencholaimellus* Cobb, 1915; *Xiphinema* Cobb, 1913; *Triplonchium* Cobb, 1920.
Subfamily Dorylaiminae.
    Genera: *Trichodorus* Cobb, 1913; *Leptonchus* Cobb, 1920 (probable synonym of *Trichodorus*); *Longidorus* Micoletzky, 1922; *Oionchus* Cobb, 1913; *Campydora* Cobb, 1920; *Sectonema* Thorne, 1930; *Nygolaimus* Cobb, 1913; *Chrysonema* Thorne, 1929; *Dorylaimus* Dujardin, 1845 (sg. *Discolaimus* Cobb, 1913; syn. *Antholaimus* Cobb, 1913; sg. *Dory-*

laimellus Cobb, 1913; sg. *Axonchium* Cobb, 1920); *Doryllium* Cobb, 1920; *Actinolaimus* Cobb, 1913.

KEY TO SUBFAMILIES OF DORYLAIMIDAE

1. (2) Buccal capsule completely toothless or absent....... **Alaiminae**
2. (1) Teeth or spear present.
3. (4) Three labial teeth present .... **Ironinae**
4. (3) A buccal spear present, simple or triple, rarely separated into three isolated rods.
5. (6) Spear triple, in *Diphtherophora* separated into three rods .... **Tylencholaiminae**
6. (5) Spear simple, short or elongated .... **Dorylaiminae**

The most characteristic feature of members of this family is their esophagus (fig. 20); it is narrow and the musculature is very weak or even quite absent anteriorly, but gradually expanded and normally formed posteriorly. Cobb had good reason to speak of a "dorylaimoid" esophagus. The sensory organs of the head are always in the form of papillae, a feature which is probably correlated with their sucking habits, as in *Mononchus*. The caudal glands and pore are absent in the fresh-water genera but present in the marine ones.

The first subfamily has no differentiated mouth structures. Whether this is a primitive feature or should be considered as a terminal stage in their reduction from previous structures is problematical. The second possibility seems to me more probable because of the general appearance of degeneration of the esophagus in some of them. The Alaiminae, with their typical dorylaimoid esophagus, might have arisen from some of the Dorylaiminae that had lost their spear. It is possible that the investigation of the larval stages will throw more light on this matter.

The characteristic feature of the Ironinae is the presence of three teeth immediately behind the lips. These teeth belong to the esophagus. In the larvae they are formed before each molt in a position posterior to the functional ones, moving forward in the course of the molts. The teeth can be everted outside the mouth, functioning as digging organs (Cobb, 1928).

The Tylencholaiminae and Dorylaiminae are characterized by the presence of protrusible spears. In the first subfamily there is a threefold spear (fig. 21) arising from the three esophageal sectors. In Dorylaiminae there is only one spear, subventral and asymmetrical in position. In *Nygolaimus* it is distinctly separate from the esophageal cuticle and simply acute (fig. 22). In *Dorylaimus* it has the form of a hollow tube cut obliquely (fig. 23), a "goose feather." The genital region of the male resembles that of *Mononchus* in having numerous papillae, tubular in some species, and a strong bursal musculature (fig. 24).

Subfamilies and Genera of the Family Mermitidae

Subfamily Tetradonematinae.

Genera: *Aproctonema* Keilin, 1917; *Tetradonema* Cobb, 1919.

Subfamily Mermitinae.

Genera: *Neomermis* Linstow, 1904 (syn. *Octomermis* Steiner, 1929); *Mermis* Dujardin, 1842; *Allomermis* Steiner, 1924; *Pseudomermis* de Man, 1904; *Tetramermis* Steiner, 1927; *Agamermis* Cobb, Steiner and Christie, 1923; *Hexamermis* Steiner, 1924; *Bathymermis* Daday, 1913; *Eumermis* Daday, 1913; *Paramermis* Linstow, 1901; *Limnomermis* Daday, 1913; *Hydromermis* Corti, 1903; *Gastromermis* Micoletzky, 1925; *Mesomermis* Daday, 1913; *Eomermis* Steiner, 1929; ?*Bolbinium* Cobb, 1920; ?*Colpurella* Cobb, 1920; ?*Isolaimium* Cobb, 1920.

KEY TO SUBFAMILIES OF MERMITIDAE

1. (2) Musculature weak; head papillae feebly developed; amphids obliterated; body soft; adult stage parasitic in midges, *Sciara* spp. .... Tetradonematinae
2. (1) Musculature, head papillae and amphids well developed; adult stage free-living .... Mermitinae

The writer agrees with Steiner (1917) who considers the Mermitidae as descendants of the Dorylaimidae. The most suggestive evidences, as expressly pointed out by him, are the presence of a tylencholaimoid spear in the larvae and the resemblance in the structure of the esophagus. Some other hints in the same direction are to be seen in the structure of the adults. On the head (fig. 26) one can clearly see the pocketlike amphid common to these forms and to the other members of the Enoplata, and absent in any other nematode group. The tail of the male (fig. 25) with its numerous preanal papillae is also similar in a general way to that of the Dorylaimidae.

There are two different groups in the family. The Tetradonematinae are parasitic until the end of their life; therefore the cuticle of the body becomes soft, and the musculature and cephalic sense organs reduced. Nevertheless they can be compared with the Mermitidae because of their elongated body, general appearance of the longitudinal chords, and especially because of their esophagus, the "tetrads" of which can be compared with the large esophageal cells of the true mermitids.

The Mermitinae were united in a lone genus, *Mermis*, until 1901, when *Paramermis* was proposed by Von Linstow. An elaborate system of water forms was proposed by Daday (1913). Steiner in the beginning of his studies rejected Daday's system, but afterwards he adopted all Daday's genera and proposed some of his own, thus elaborating the existing system. Dr. G. Steiner has in preparation a complete monograph of the family. Some of Cobb's genera are assigned here with some doubt.

Order CHROMADORATA

A smooth cuticle was given as one of the characteristic features in the Enoplata; a coarsely striated one, nearly always typically thickened behind the head, is characteristic for the Chromadorata. The amphid, as in the following order, is primarily spiral, the few exceptions being mostly easily explainable. The ovaries are curved as in the Enoplata. A very characteristic tail (cf. figs, 47, 48) with a long terminal tube is present in most genera. Esophageal bulbs are very common but are not present in all forms. The wide attachment of the esophagus to the cuticle is lost except in one form (*Dermatolaimus*). The six anterior cephalic setae are very often transformed into papillae, so that only the four of the posterior circle are retained as setae.

KEY TO FAMILIES OF CHROMADORATA

1. (4) Mouth capsule irreversible, mouth organs very simple, vestibulum unfolded.
2. (3) Bulb absent; the mouth surrounded by a thickening of cuticle; amphids placed far anteriorly. **Camacolaimidae**
3. (2) Bulb present; the circumoral cuticular thickening absent; amphids placed somewhat more posteriorly .... **Plectidae**
4. (1) Mouth capsule eversible, with a folded vestibulum, mostly with a dorsal tooth (with secondary complication of buccal organs—teeth, jaws, spines—in one subfamily) .... **Chromadoridae**

GENERA OF THE FAMILY CAMACOLAIMIDAE

Genera: *Camacolaimus* de Man, 1889 (syn. *Acontiolaimus* Filipjev, 1918; syn. *Digitonchus* Cobb, 1920; syn. *Ypsilon* Cobb, 1920); *Neurella* Cobb, 1920; *Halaphanolaimus* Southern, 1914; *Dermatolaimus* Steiner, 1916; *Stephanolaimus* Ditlevsen, 1919; *Alaimella* Cobb, 1920; *Nemella* Cobb, 1920; *Onchium* Cobb, 1920; *Onchulella* Cobb, 1920; *Ionema* Cobb, 1920; *Cricolaimus* Southern, 1914; *Dagda* Southern, 1914; *Aphanolaimus* de Man, 1880; *Paraphanolaimus* Micoletzky, 1923; *Iotalaimus* Cobb, 1920; *Basti-*

ania de Man, 1876; *Dintheria* de Man, 1922; *Deontolaimus* de Man, 1880; *Leptolaimus* de Man, 1876; *Conolaimella* Allgén, 1930; *Antomicron* Cobb, 1920; *Cynura* Cobb, 1920; *Polylaimium* Cobb, 1920.

This family should be regarded as the most primitive one in the order. The cuticle is somewhat thickened around the mouth opening, and the esophagus is attached to this thickening by a narrow strip (fig. 27), this simple arrangement being realized in all genera without any complications. The amphids are mostly spiral-shaped and in a forward position. Most of the genera are marine, but some are fresh-water, rarely soil, nematodes.

Dermatolaimus is one of the simplest members of the family (fig. 28). It is the single member of the order with a more or less extensive attachment of the esophagus to the cuticle; this is possibly due to the reduction of the musculature in the anterior part of the former. There is no differentiation in the mouth structures. The latter are complicated in *Camacolaimus* and in some other genera by the formation of spears that seem to be protrusible. In the fresh-water genus *Aphanolaimus* there is a complete absence of differentiated mouth structures; the amphids are rounded with a bubblelike median swelling (figs. 29, 30). The closely related *Paraphanolaimus* has typical spiral amphids. In young specimens of *Aphanolaimus* the writer has seen on the larval skin a true spiral amphid and a typical swollen one under it. The preanal tubes are peculiar to that genus and are very similar to that of some species of *Plectus,* thus giving a connecting link to the following family.

GENERA OF THE FAMILY PLECTIDAE

Genera: *Plectus* Bastian, 1865; *Pycnolaimus* Cobb, 1920; *Haliplectus* Cobb, 1913; *Wilsonema* Cobb, 1913; *Anthonema* Cobb, 1906; *Aulolaimoides* Micoletzky, 1917; *Chronogaster* Cobb, 1913; *Paraplectus* Filipjev, 1929; *Rhabdolaimus* de Man, 1880; *Isolaimium* Cobb, 1920; *Tripylium* Cobb, 1920; *Walcherenia* de Man, 1922c; *Pseudobathylaimus* Filipjev, 1918 (syn. *Bathylaimus* Daday, 1905, preocc.; syn. *Dadaya* Micoletzky, 1922); *Paradoxolaimus* Kreis, 1924; *Pseudochromadora* Daday, 1900; *Aplectus* Cobb, 1914; *Diodontolaimus* Southern, 1914.

This family, like the foregoing one, has irreversible mouth organs, but the circumoral thickening of the cuticle is not so pronounced. The difference between the two is in the complication of the inner esophageal tube; this is simple in the Camacolaimidae, but in the Plectidae it forms ordinarily a well-isolated buccal capsule anteriorly, followed by a valvular constriction, and with a dilatation inside the well-developed bulbus, with or without masticatory plates.

The Plectidae are mostly terrestrial or fresh-water nematodes with only a very few marine genera. All genera have prominent spiral amphids of somewhat aberrant type in a posterior position (fig. 27). In the tail there are caudal glands and spinneret; the tail is mostly of the typical chromadoroid form. Many forms are interesting biologically on account of their ability to revive after complete desiccation. The generic analysis of this group seems to be as yet far from being finished.

Subfamilies and Genera of the Family Chromadoridae

Subfamily Cyatholaiminae.

Genera: *Necticonema* Marion, 1870; *Cyatholaimus* Bastian, 1865; *Praeacanthonchus* Micoletzky, 1924; *Seuratiella* Ditlevsen, 1921 (syn. *Seuratia* Ditlevsen, 1919, preocc.); *Paracanthonchus* Micoletzky, 1924; *Acanthonchus* Cobb, 1920; *Paracyatholaimus* Micoletzky, 1924; *Longicyatholaimus* Micoletzky, 1924; *Statenia* Allgén, 1930; *Nannonchus* Cobb, 1913; *Achromadora* Cobb, 1913; *Pomponema* Cobb, 1917; *Nannolaimus* Cobb, 1920; *Ethmolaimus* de Man, 1880; *Odontolaimus* de Man, 1880; *Prodesmodora* Micoletzky, 1923; *Anatonchium* Cobb, 1920.

Subfamily Choanolaiminae.

Genera: *Demonema* Cobb, 1893; *Bulbopharyngiella* Allgén, 1929; *Chonialaimus* Ditlevsen, 1919; *Cobbionema* Filipjev, 1922; *Zygonemella* Cobb, 1920; *Zalonema* Cobb, 1920; *Choanolaimus* de Man, 1880: *Anonchus* Cobb, 1913; *Halichoanolaimus* de Man, 1886; *Smallsundia* Allgén, 1929; *Gammanema* Cobb, 1920; *Trogolaimus* Cobb, 1920; *Selachinema* Cobb, 1915; *Pseudonchus* Cobb, 1920; *Synonchium* Cobb, 1920; *Cheironchus* Cobb, 1917 (syn. *Dignathonema* Filipjev, 1918).

Subfamily Richtersiinae.

Genera: *Richtersia* Steiner, 1916; *Richtersiella* Kreis, 1929.

Subfamily Chromadorinae.[2]

Genera: *Euchromadora* de Man, 1886; *Odontocricus* Steiner, 1918; *Dicriconema* Steiner and Hoeppli, 1926; *Rhabdotoderma* Marion, 1870; *Fusonema* Kreis, 1928; *Actinonema* Cobb, 1920; *Rhips* Cobb, 1920; *Neochromadora* Micoletzky, 1924; *Prochromadora* Filipjev, 1922; *Prochromadorella* Micoletzky, 1924; *Spiliphera* Bastian, 1865; *Deltanema* Kreis, 1929; *Chromadorina* Filipjev, 1918; *Chromadorella* Filipjev, 1918; *Spilophorella* Filipjev, 1918; *Chromadorissa* Filipjev, 1917; *Graphonema* Cobb, 1898; *Punctodora* Filipjev, 1929; *Hypodontolaimus* de Man, 1886 (syn. *Iotadorus* Cobb, 1920); *Ptycholaimellus* Cobb, 1920; *Oistolaimus* Ditlevsen, 1921; *Odontonema* Filipjev, 1929; *Endolaimus* Filipjev, 1922; *Chromadorita* Filipjev, 1922.

Subfamily Desmodorinae.

Genera: *Desmodora* de Man, 1889; *Amphispira* Cobb, 1920; *Xenonema* Cobb, 1920; *Bolbonema* Cobb, 1920; *Micromicron* Cobb, 1920; *Eute-*

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[2] Kreis (1929) proposed some generic or subgeneric groups, for which he did not propose types, as follows: *Macrochromadora* (for a part of *Prochromadorella*); *Dichromadora, Trichromadora* (for parts of *Chromadora*); *Chromarina* (possibly synonymous with *Punctodora*).

lolaimus de Man, 1922; *Antomicron* Cobb, 1920; *Mastodex* Steiner, 1921; *Aculeonchus* Kreis, 1928; *Heterodesmodora* Micoletzky, 1924;
10. *Stilbonema* Cobb, 1920; *Laxonema* Cobb, 1920; *Leptonemella* Cobb, 1920; *Croconema* Cobb, 1920; *Metachromadora* Filipjev, 1918 (syn. *Chromadoropsis* Filipjev, 1918); *Xanthodora* Cobb, 1920; *Onyx* Cobb, 1891; *Acanthopharynx* Marion, 1870; *Cinctonema* Cobb, 1920; *Chromaspirina* Filipjev, 1918 (syn. *Mesodorus* Cobb, 1920); *Polysigma* Cobb, 1920; *Laxus* Cobb, 1893; *Parathalassoalaimus* Allgén, 1929; *Catanema* Cobb, 1920; *Spirina* Filipjev, 1918 (syn. *Spira* Bastian, 1865, preocc.).

Subfamily Monoposthiinae.

Genera: *Monoposthia* de Man, 1889; *Xenolaimus* Cobb, 1920; *Dasynema* Cobb, 1920; *Nudora* Cobb, 1920; *Rhinema* Cobb, 1920; *?Ceramonema* Cobb, 1920 (syn. *Steineria* Filipjev, 1922, preocc.).

Subfamily Epsilonematinae.

Genera: *Prochaetosoma* Baylis and Daubney, 1926 (syn. *Rhabdogaster* Metchnikov, 1867, preocc.); *Epsilonema* Steiner, 1926; *Metepsilonema* Steiner, 1926.

Subfamily Draconematinae.

Genera: *Notochaetosoma* Irwin-Smith, 1918; *Draconema* Cobb, 1913; *Tristicochaeta* Panceri, 1876; *Claparediella,* nom. nov. (*Chaetosoma* Claparède, 1863, preocc.).

KEY TO THE SUBFAMILIES OF CHROMADORIDAE

1. (8) The cuticular rings with inner spots or dots or short external setae.
2. (7) Amphids located at some distance from the head end, well developed, spiral or roundish. Esophagus usually strong and without bulb.
3. (6) Cuticle without setae, except the ordinary setae; the annules not prominent.
4. (5) Mouth capsule typical, preceded by a folded vestibulum and with a dorsal onchium .... Cyatholaiminae
5. (4) Mouth capsule atypical, very differently built up, with peculiar plates, bristles, jaws, etc., serving for retaining prey. Mostly rapacious marine forms. .... Choanolaiminae
6. (3) Cuticle with numerous short setae; body very short .... Richtersiinae
7. (2) Amphids located close to the head end, in some genera obsolete, in form of a transverse slit. Cuticular rings sharply differentiated. Esophagus usually with a well-developed bulb. Mostly small forms .... Chromadorinae
8. (1) The cuticular annules smooth.
9. (12) Without adhesive setae.
10. (11) Without any longitudinal, cuticular crests (except lateral wings in some) .... Desmodorinae

11. (10) With sharp, longitudinal, cuticular crests along the body (differentiated in some as rows of spines). **Monoposthiinae**
12. (9) Special adhesive setae present in two groups, some on the head and some in two or more rows in preanal position.
13. (14) Adhesive setae in form of hooks without a hollow interior .... **Epsilonematinae**
14. (13) Adhesive setae in form of hollow tubes ...... **Draconematinae**

The chief distinction between the Chromadoridae and the two other families is in the eversible mouth capsule of this family. In connection with this the vestibulum becomes twelvefold and composed of a soft pliable cuticle. The body cuticle around the mouth also presents a soft portion, the reverse of the cuticular thickening in Plectidae. In all typical forms there is a more or less developed dorsal onchium in the mouth capsule (figs. 31, 32). When the latter is everted, the tooth points forward and functions as an incising or picking organ. Sometimes the tooth is strongly developed and presents a kind of spear, compared by some authors with that of the Dorylaiminae, but its general form and position, dorsal instead of subventral as in the latter, do not permit of considering the two as homologous organs. This typical organization is not clear in the Choanolaiminae where the mouth structures are much more complex. In the Desmodorinae several genera show a reduction of the buccal tooth in size, and in some others it may disappear completely. The folds of the soft cuticle around the unarmed mouth of such forms are the only remains of the typical conditions.

The Cyatholaiminae (figs. 31, 32) have typical spiral amphids, generally with many turns, and a cuticle with very plain rings and transverse rows of points inside. The esophagus is broad, uniform for its full length, and without a bulb except in the somewhat aberrant fresh-water genera *Ethmolaimus, Prodesmodora,* and *Achromadora,* but the characteristic inner cavity of true bulbs is lacking in these genera. There are 10 cephalic setae in all genera.

An offshoot of the Cyatholaiminae are the Choanolaiminae, a group of predacious genera, nearly all marine, with the same cuticle, amphids, and tail as in the true Cyatholaiminae (figs. 33–40). Very characteristic are the large cells of the intestine. The mouth structures are specialized in several directions. In *Halichoanolaimus* there are six true lips and a complex mouth capsule with rows of spines in the form of a comb to retain the nematode's prey inside (figs. 33–35). In *Cheironchus* there are two jaws (figs. 36–38), very similar to those of *Enoplus*. *Synonchium* (figs. 39–40) has three of them, quite as in *Enoplus,* but it is, of course, nothing other than a very evident case of convergence, no other character being like that genus, whereas many characters resemble *Cyatholaimus* or the other Choanolaiminae.

The peculiar genus *Richtersia* (fig. 41) with its setaceous cuticle shows similarities in its esophagus, its cuticle with the points, and its spiral amphids, with the Cyatholaiminae, but it is advisable to place it in a separate subfamily.

A very large number of species, nearly infinite in their diversity, must be included in the subfamily Chromadorinae. They are mostly small and very variable in the structure of the cuticle, mouth capsule and esophagus. All have only four cephalic setae and nearly all a bulb and preanal papillae giving good diagnostic characters for different species. The amphid in some forms is a typical little spiral lying very far forward (fig. 42), in others the abbreviation of the head flattens the spiral which thus becomes the slitlike amphid typical for these other genera (fig. 43).

The forms with the plain ringed cuticle consist of several subfamilies. The Desmodorinae have ordinary plain annules, without any complications, and spiral amphids. The cuticle of the head is generally strong and smooth, except in a few genera like *Metachromadora* and *Onyx* which have a striation independent of that of the body (fig. 44). *Onyx* has also a strongly developed spearlike tooth and 12 well-isolated lips.

The Monoposthiinae are characterized by a peculiar cuticle with longitudinal rows of spines, in some forms fused into continuous wings (fig. 45). Usually there is a round amphid, although several forms have a spiral one. A very peculiar genus is *Ceramonema,* placed here provisionally because of its cuticular rings (fig. 46). The rings are very prominent and the amphid is horseshoe-shaped instead of being spiral. The reduction of the mouth parts and a very feeble onchium and buccal musculature should also be noted.

The last two subfamilies are treated by many authors as a separate family or even an order, so aberrant are they in a general view. Chaetosomatidae is the name most used for them, but *Chaetosoma* being preoccupied, that family name also falls. The most remarkable feature is the general form of the body with the swollen esophageal part generally called the "head" followed by the thin "neck" (figs. 47, 48), but the same form of the body, although not so well developed, is found in several members of the Desmodorinae. The coarse, plain striation of the cuticle, coarser behind the head, is a common character of all of the latter. The horseshoe-shaped amphid is quite like that of *Ceramonema*. The tail is typically chromadoroid, the spicules similar to those of *Desmodora*. The esophagus of *Draconema* with its two swellings is quite distinctive, but *Notochaetosoma* has an ordinary unibulbar esophagus. The adhesive setae of these forms, concentrated in two regions, on the head and in the preanal region, are peculiar. Steiner (1926) proposes to treat the Epsilonematidae (fig. 47), with the solid adhesive setae, separately from the Draconematidae, with the tubular ones each connected with a gland which is probably a cement gland. Although agreeing with his principal idea, the writer could hardly ascribe to them a rank more elevated than that of a subfamily, the close connection with the Desmodorinae not justifying their separation.

Order DESMOSCOLECATA

FAMILIES AND GENERA OF DESMOSCOLECATA

Family Desmoscolecidae.
  Genera: *Eudesmoscolex* Steiner, 1916; *Desmoscolex* Claparède, 1863; *Quadricoma* Filipjev, 1922; *Tricoma* Cobb, 1893.
Family Greeffiellidae.
  Genus: *Greeffiella* Cobb, 1922 (syn. *Trichoderma* Greeff, 1869, preocc.).

KEY TO FAMILIES OF DESMOSCOLECATA

1. (2) Setae not very numerous, body having a naked appearance. Secreted rings usually present ..**Desmoscolecidae**
2. (1) Setae and nerveless spines very numerous, the body having a hairy appearance. Secreted rings absent .... **Greeffiellidae**

This order includes a group, comparatively small as yet, of marine forms. The most characteristic feature is their cuticle with its very prominent chitinous rings, from 12 to nearly 84 in number. They have the appearance of body segments and have led to a comparison of these forms with the annelids, but they are purely external or even secreted, having no relation to the internal organs (figs. 49, 50). The large amphids are very prominent. The strong setae of the body constitute a development in connection with the peculiar mode of locomotion, the nematodes traveling on them as on stilts, the dorsal side downward. Interesting also is the habit of bearing the eggs fastened on the outside of the female body. Very little is known about the inner organization of these forms, not even whether they have straight or reflexed ovaries. It is a very isolated group with a somewhat uncertain systematic position.

The genus *Greeffiella* is composed of distinctive setaceous, mostly exceedingly minute species. The head is similar to that of the Desmoscolecidae, but they must form a quite separate family.

Order MONHYSTERATA

Under this name are united all the true free-living forms with the straight (not reflexed) ovaries (fig. 51). The amphids are always very distinct and either spiral, horseshoe-shaped, or circular, the last type probably being a reduced spiral. The other morphological characters are very inconstant. The cuticle is mostly striated, but in some forms smooth. The esophagus is usually without a bulb. The vestibulum is well developed, with a chitinous ring on the bottom which serves as a support to the esophagus (fig. 52). This ring is lacking, probably lost, in most of the Linhomoeidae. Very often there is a strengthening of the vestibulum by means of several chitinous rods inside its walls (figs. 52, 53); these rods are sometimes separated from the walls and can spread forward or sideward when the mouth is open. In spite of the meager morphological characteristics of the group, there are very gradual transitions between its different members, so that it seems to be a very natural one.

KEY TO FAMILIES OF MONHYSTERATA

1. (2) Spicules short and strong, distinctly bent to form an arch (rarely double), with a strong gubernaculum guiding their ends and armed with two obliquely backward-pointing processes serving to attach muscles .... **Linhomoeidae**
2. (1) Spicules short or long, with a gubernaculum without backward-pointing processes, or with feebly developed ones .... **Monhysteridae**

SUBFAMILIES AND GENERA OF THE FAMILY MONHYSTERIDAE

Subfamily Monhysterinae.

Genera: *Paramonhystera* Steiner, 1916; *Amphimonhystera* Allgén, 1929; *?Porocoma* Cobb, 1920; *Penzancia* de Man, 1889; *Theristus* Bastian, 1865 (syn. *Allomonhystera* Micoletzky, 1923); *Daptonema* Cobb, 1920; *Tubolaimus* Allgén, 1929; *Monhystrium* Cobb, 1920; *Cobbia* de Man, 1907; *Gonionchus* Cobb, 1920; *?Xyala* Cobb, 1920; *?Rhynchonema* Cobb, 1920; *Dactylaimus* Cobb, 1920; *Microlaimus* de Man, 1880; *?Bolbolaimus* Cobb, 1920; *Monhystera* Bastian, 1865 (syn. *Tachyhodites* Bastian, 1865); *Diplolaimella* Allgén, 1929; *Monohystrella* Cobb, 1918; *Scaptrella* Cobb, 1917; *Austronema* Cobb, 1914; *Leptogastrella* Cobb, 1920; *Omicronema* Cobb, 1920; *Cylindrolaimus* de Man, 1880.

Subfamily Sphaerolaiminae.

Genera: *Crassolaimus* Kreis, 1929; *Sphaerolaimus* Bastian, 1865; *Parasphaerolaimus* Ditlevsen, 1919; *?Cytolaimium* Cobb, 1920.

Subfamily Comesominae.

Genera: *Comesoma* Bastian, 1865; *Laimella* Cobb, 1920; *Dentatonema* Kreis, 1928.

KEY TO SUBFAMILIES OF MONHYSTERIDAE

1. (4) Amphids roundish.
2. (3) Mouth capsule variable, but never with thick walls or free .... **Monhysterinae**
3. (2) Mouth capsule with thick chitinized walls, partly free and adjoining the cuticle of the head...**Sphaerolaiminae**
4. (1) Amphids spiral in several windings .... **Comesominae**

The Monhysteridae possess as a rule only one ovary, the anterior one (fig. 51); in relation with this the vulva is situated very far backward. The above mentioned chitinous ring of the vestibulum is well developed; in Sphaerolaiminae it is enlarged and forms a spacious mouth capsule (fig. 53). The amphids are round or spiral (Comesominae, fig. 54); the round form seems to be a secondary one, arising from the spiral by the reduction of its inner coils. The spicules are long or short. The gubernaculum is generally well developed, sometimes with a backward-pointing process, but never so strongly developed as in the following family.

SUBFAMILIES AND GENERA OF THE FAMILY LINHOMOEIDAE

Subfamily Linhomoeinae.

Genera: *?Litotes* Cobb, 1920; *Linhomoeus* Bastian, 1865 (sg. *Eulinhomoeus* de Man, 1907; sg. *Paralinhomoeus* de Man, 1907; syn. *Anticyclus* Cobb, 1920); *Rhadinema* Cobb, 1920; *Monhysteriella* Kreis, 1929; *Crystallonema* Cobb, 1920; *Odontobius* Roussel de Vauzème, 1834; *Linhomoella* Cobb, 1920; *Metalaimus* Kreis, 1928; *Metalinhomoeus* de Man, 1907; *Prosphaerolaimus* Filipjev, 1918 (syn. *Anticyathus* Cobb, 1920); *Synonema* Cobb, 1920; *Desmolaimus* de Man, 1880; *Terschellingia* de Man, 1888; *Aegialoalaimus* de Man, 1907; *Eleutherolaimus* Filipjev, 1922; *Oligomonhystera* Micoletzky, 1922; *Zanema* Cobb, 1920; *Chloronemella* Allgén, 1929; *Halinema* Cobb, 1920; *Rhinonema* Allgén, 1927; *Solenolaimus* Cobb, 1893 (syn. *Anthraconema* Zur Strassen, 1904); *Siphonolaimus* de Man, 1893 (syn. *Chromagaster* Cobb, 1893); *Southernia* Allgén, 1929; *Cyartonema* Cobb, 1920; *Disconema* Filipjev, 1918.

Subfamily Axonolaiminae.

Genera: *Margonema* Cobb, 1920; *Fimbriella* Allgén, 1929; *Axonolaimus* de Man, 1889; *Synodontium* Cobb, 1920; *Ascolaimus* Ditlevsen, 1919 (syn. *Bathylaimus* Ditlevsen, 1919, preocc.); *Apodontium* Cobb, 1920; *Odontophora* Bütschli, 1874 (syn. *Conolaimus* Filipjev, 1918; syn. *Trigonolaimus* Ditlevsen, 1919); *Synonema* Cobb, 1920; *Araeolaimus* de Man, 1888; *Conolaimella* Allgén, 1930; *Araeolaimoides* de Man, 1893; *Coinonema* Cobb, 1920; *Diplopeltis* Cobb, 1905 (syn. *Discophora*

Villot, 1876, preocc.; syn. *Dipeltis* Cobb, 1891, preocc.); *Didelta* Cobb, 1920; *Acmaeolaimus* Filipjev, 1918; *Sphaerocephalum* Filipjev, 1918; *Aponchium* Cobb, 1920; *?Campylaimus* Cobb, 1920; *?Pseudolella* Cobb, 1920.

Subfamily Sabatieriinae.

Genera: *Sabatieria* Rouville, 1903 (syn. *Parasabatieria* de Man, 1907); *Kreisia* Allgén, 1929; *Alaimonema* Cobb, 1920; *Pepsonema* Cobb, 1920; *Mesonchium* Cobb, 1920; *Dorylaimopsis* Ditlevsen, 1919 (syn. *Xinema* Cobb, 1920); *Filipjeva* Ditlevsen, 1926.

KEY TO SUBFAMILIES OF LINHOMOEIDAE

1. (2, 3) Amphids roundish, i.e., spiral in one winding. . **Linhomoeinae**
2. (1, 3) Amphids horseshoe-shaped, oval, or roundish in general shape, sometimes on a specially differentiated cuticular plate; in several genera both ends of the horseshoe come so near together as to touch each other (the amphid can then easily be mistaken for a spiral one) .... **Axonolaiminae**
3. (1, 2) Amphids spiral in several windings .... **Sabatieriinae**

This family is different in many respects from the Monhysteridae. The cuticle is never so coarsely striated as in many members of the Monhysteridae; it is always very soft and pliable, mostly with a very fine striation or plain. The head is rounded and the mouth is formed as in the Monhysteridae, but the chitinous ring conspicuous in monhysterids is less prominent or sometimes quite obliterated (fig. 55). The most characteristic features are the spicules, strongly curved and accompanied by a double backward-pointing gubernaculum (fig. 56). In some genera the spicules are double but with the same gubernaculum (figs. 57, 58). The division of the group into subfamilies is based chiefly on the form of the amphids. In the Linhomoeinae the amphid is roundish, and an oblique incision of its border reveals its true nature as a spiral of a little more than one turn. The manner of their origin seems also to be different from that in the Monhysteridae. In the Axonolaiminae the amphids have the form of a bent horseshoe, an elongated oval, as a rule, or are roundish (fig. 59); it is probable that this form is to be considered as more primitive even than the spiral one. In *Diplopeltis* this horseshoe is supported by a special chitinous plate (fig. 60). In the Sabatieriinae the amphid is a regular spiral in several turns, very similar to that of the Comesominae, but the spicules afford a very good distinguishing character for the two groups.

Herewith we come to the end of the typical free Nematoda.

There are to be noted among them some transitions to the parasitic life. The impulse was certainly given by the peculiar semiparasitic feeding habits of many of them, sucking on the body of other larger animals. Thus some *Phanoderma*-like nematodes were found by Ditlevsen (1927) partly buried in the body of Polychaeta. The writer (Filipjev, 1927) found a *Phanodermopsis* with the musculature of the esophagus and nearly all other organs degenerated and apparently not functional except for the genitalia, which also gives a hint of their parasitic nature. *Solenolaimus* and *Siphonolaimus* have a very dark reddish intestine which is explained by Zur Strassen as resulting from their feeding on polychaete worms. The writer found in Neva Bay *Dorylaimus stagnalis* with the intestine colored quite as are the Oligochaeta in the same habitats. The entire group of Mermitidae passes most of its larval life and all the time of feeding inside insects or some other invertebrates. *Odontobius ceti,* a linhomoeid, is found, according to Baylis, in the mouth of whales, although rather in saprozoic than in parasitic conditions. The soft cuticle of all Linhomoeidae suggests that they may be liberated from a host after the fashion of the Mermitidae. It would not be surprising if the young or larvae of some parasites, especially those of marine fishes, would be found very like some free-living marine genera, thus giving a key to the phylogeny of certain parasitic groups.

The same idea was recently expressed by Wülker (1929) but probably he was not entirely happy in the material selected for comparison (cf. pp. 195–196).

Order ANGUILLULATA

As has been said, most of the saprozoic and terricolous forms of this order are very different from the foregoing groups in their physiology. The cuticle is very impermeable and does not allow the substances of the external medium to penetrate. This explains the strange fact that many forms of this order can live for hours in such fluids as corrosive sublimate, formaldehyde or osmic solutions capable of killing other animals in a few seconds. The ordinary vinegar eel lives even normally in a medium that would be fatal for most other animals. Possibly it is the same lipoid cover that was investigated by Zavadovsky in the eggs of Ascaris that preserves these forms.

One of the features of this order is the absence in nearly all of them of the setae on the head and the whole body, these being replaced by papillae; generally the latter are not very prominent aside from the genital papillae of the male. The amphids have a very reduced size and their existence was established with certainty only within the last few years; externally they are represented by inconspicuous slits or even papillae. The caudal glands are absent; they are replaced in some, if not in all, forms by paired subcaudal glands opening on the sides of the tail; they are probably not homologous with the true caudal glands. In the esophagus there is often a bulb with the masticatory apparatus inside; a preneural swelling is present in several forms (fig. 61); in others it is transformed into a true second bulb, generally called the middle bulb, the posterior or cardiac bulb corresponding to that of the other forms (fig. 65); in still others the musculature is much reduced in the posterior bulb, only the glandular cells being preserved, the only muscular bulb being the anterior one (fig. 67). In *Aphelenchus* and some other genera the cells of the posterior glandular part of the esophagus are not separated from the intestine by any constriction, so that it appears as though the neural ring is situated around the anterior part of the intestine. In the male genitalia there is often a prominent bursa (figs. 62, 63). The whole organization bears traces of reduction and definitiveness; the musculature is mostly meromyarian: a sacrifice to the accelerated development characteristic of and indispensable to these saprozoic forms. There seems to be no group in the families previously discussed to which the organization of this order could be closely compared with good reason.

KEY TO FAMILIES OF ANGUILLULATA

1. (4) Esophagus with or without a bulb. Free-living or parasites of plants and insects.
2. (3) Esophagus with the cardiac bulb .... **Anguillulidae**
3. (2) Esophagus with the middle bulb present or reduced .... **Tylenchidae**
4 (1) Esophagus without bulb, of uniform musculature throughout its length. Parasites of vertebrates.
5. (6) Syngonic; digenetic with a free-living rhabditoid generation .... **Anguillulidae** (partim)
6. (5) Amphigonic; with direct development, rhabditoid larvae never reaching free-living maturity. ....**Strongylidae**

Subfamilies and Genera of the Family Anguillulidae

Subfamily Anguillulinae.

Genera: *Rhabditis* Dujardin, 1845 (sg. *Rhabditella* Cobb, 1929); *Rhabditoides* Goodey, 1929; *Asymmetricus* Kreis, 1930 (syn. *Pseudorhabditis* Kreis, 1929, preocc.); *Diploscapter* Cobb, 1913; *Hyalaimus* Cobb, 1920.

Subfamily Steinerneminae.

Genera: *Neoaplectana* Steiner, 1929; *Steinernema* Travassos, 1927c (syn. *Steineria* Travassos, 1927a, preocc.); *Hemicycliophora* de Man, 1921; *Cheilobus* Cobb, 1924; *Anguillula* C. F. Mueller, 1783 (syn. *Turbatrix* Peters, 1927); *Macrolaimus* Maupas, 1900; *Myolaimus* Cobb, 1920; *Himatidiophila* Rahm, 1924.

Subfamily Cephalobinae.

Genera: *Cephalobus* Bastian, 1865 (syn. *Plectonchus* Fuchs, 1930; sg. *Neocephalobus* Steiner, 1929); *Aloinema* A. Schneider, 1859; *Rhabditophanes* Fuchs, 1930; *Panagrolaimus* Fuchs, 1930; *Poikilolaimus* Fuchs, 1930; *Diastolaimus* Rahm, 1930; *Acrobeloides* Cobb, 1924; *Acrobeles* Linstow, 1877; *Plectonchus* Fuchs, 1930; *Chambersiella* Cobb, 1920; *Panagrolaimus* Fuchs, 1930; *Teratocephalus* de Man, 1876 (syn. *?Mitrephoros* Linstow, 1877); *? Choronema* Cobb, 1920.

Subfamily Cephalobiinae.

Genus: *Cephalobium* Cobb, 1920. The objections of Peters to the use of the old name, well established and universally used since Bastian, are at least questionable. Even if they should prove to be valid, an exception to the rules of priority should be made for this case.

Subfamily Bunoneminae.

Genera: *Bunonema* Jägerskiöld, 1905; *Craspedonema* Richters, 1908; *Rhodolaimus* Fuchs, 1930.

Subfamily Rhabdiasinae.

Genera: *Rhabdias* Stiles and Hassall, 1905 (syn. *Rhabdonema* Leuckart, 1879, preocc.); *Strongyloides* Grassi, 1879 (syn. *Pseudorhabditis* Perroncito, 1880; syn. *Stercoralis* Tanaka, 1910).

KEY TO SUBFAMILIES OF ANGUILLULIDAE

1. (9) Free-living or saprozoic forms; monogenetic. The cardiac bulb developed, with masticatory plates.
2. (5) No special differentiation of the cuticle (aside from lateral wings and the male bursa in some forms).
3. (4) The large part of the wall of the mouth capsule consisting of only one ring of chitinous plates. **Anguillulinae**
4. (3) The wall of the mouth capsule consisting of several rings of plates with a thinner cuticle between them .... **Cephalobinae**
5. (2) Cuticle with peculiar differentiations, such as asymmetrical knobs, wings, or similar things ...... **Bunoneminae**
6. (9) Parasites of insects.
7. (8) Parasites of the body cavity of insects. Body enlarged with a spacious body cavity .... **Steinerneminae**
8. (7) Parasites of the intestine. Body filiform without a large body cavity .... **Cephalobiniinae**
9. (6) Digenetic: the free-living generation very like, sometimes indistinguishable from, the Anguillulinae; the parasite generation consisting of syngonic females only, with a uniform muscular esophagus .... **Rhabdiasinae**

In this family are united all the forms showing a simple esophagus as in most other nematodes, i.e., without a division into anterior muscular and posterior glandular portion as in the following family. The free-living saprozoic forms have a very characteristic cardiac bulb with masticatory plates inside, which is always the chief, or at least an important, part of the muscular esophageal pump. The preneural esophageal swelling is present in most forms, less conspicuous, and sometimes undeveloped, in Anguillulinae, always very prominent in Cephalobinae. The Anguillulinae are the most simple forms, generally with an elongated, unarmed, well-developed buccal capsule (fig. 61); it is probable that some forms with a narrow buccal capsule acquired this secondarily. It is very probable that most earthworm parasites should be annexed to the Anguillulinae.[3]

Besides the distinction mentioned in the structure of the esophagus, there is another in the structure of the mouth capsule. In the Anguillulinae its walls are for the most part built up of three parallel uninterrupted plates. In the Cephalobinae there are several such plates with a thinner cuticle between them. It is probable that the chief plate of the Anguillulinae is homologous with only one plate of the Cephalobinae; thus the mouth capsules of the two are not homologous to each other.

The peculiar genus *Cephalobium* Cobb, parasites of the intestine of Gryllidae, could be compared, from the tooth of the mouth capsule and the preneural dilatation of the esophagus, with the Diplogasterinae, but the muscular posterior part of the esophagus makes this inclusion impossible. Therefore, the right place should be found among the Anguillulidae. The several peculiarities of structure make impossible the direct inclusion of it in the Cephalobinae, to which it can be compared, and it requires a separate subfamily. I do not find the position among the oxyurids proposed by Artigas (1929) satisfactory. The body cavity parasites, Steinerneminae, are better placed here than in the Oxyurids as proposed by Steiner.

The little group of the Bunoneminae is very closely related to the Anguillulinae. They are all moss-inhabiting species with two rows of remarkable, asymmetrical, cuticular knobs on one side of the body which thus becomes physiologically a ventral side, or other differentiations of the cuticle, often of very strange appearance, and with cephalic outgrowths (fig. 66).

Here should be placed the digenetic Rhabdiasinae, parasites of vertebrates. Baylis and Daubney gave them a place in the same sub-

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[3] The nematodes of earthworms are too little known to be included in the list directly. According to Pierantoni, they constitute a separate family, the Drilonemidae Baylis and Daubney, 1926 (syn. Cephalonemidae Pierantoni). The genera reported are: *Drilonema* Pierantoni, 1916; *Mesonema* Pierantoni, 1916; *Opistonema* Pierantoni, 1916; *Pierantonia* Baylis and Daubney, 1926 (syn. *Cephalonema* Pierantoni, 1916, preocc.); *Pharyngonema* Pierantoni, 1923; *Dicelis* Dujardin, 1845 (cf. Wülker, 1926); *Synoeconema* Magalhães, 1905 (syn. *Dionyx* Perrier, 1881, preocc.). There must be added as a doubtful genus *Lumbricicola* Friedländer, 1895 (probably young *Rhabditis* larvae).

family as the free-living genera, because of the close resemblance of their free-living bisexual generation to the free-living forms. Systematically, however, this seems to be untenable, because the syngonic parasitic generation is widely different, although there are traces of the anterior bulb in some species in this stage also (fig. 69). The free-living generation has the typical rhabditoid esophagus as in other free-living forms; the parasitic generation has a simpler esophagus without swellings or bulbs, muscular throughout its length. In some species there are traces of the anterior bulb in this stage also (fig. 69). Some species can entirely omit a free-living generation and thereby lose all hints as to their true systematic position.

Subfamilies and Genera of the Family Tylenchidae

Subfamily Diplogasterinae.

Genera: *Aulolaimus* de Man, 1880 (syn. *Myctolaimus* Cobb, 1920; syn. *Cylindrogaster* Goodey, 1927); *Rhabditidoides* Rahm, 1930; *Rhabditolaimus* Fuchs, 1915; *Neodiplogaster* Cobb, 1924 (syn. *Tylenchodon* Fuchs, 1930); *Diplogasteroides* de Man, 1912; *Lycolaimus* Rahm, 1930; *Loxolaimus* Rahm, 1930; *Diploscapteroides* Rahm, 1930; *Butlerius* Goodey, 1930; *Demaniella* Steiner, 1914; *Acrostichus* Rahm, 1930; *Diplogaster* M. Schultze, 1859; *Peronilaimus* Rahm, 1930; *Mononchoides* Rahm, 1930; *Odontopharynx* de Man, 1912; *?Ungella* Cobb, 1928; *?Scolecophilus* Baylis and Daubney, 1922.

Subfamily Tylopharynginae.

Genus: *Tylopharynx* de Man, 1876.

Subfamily Tylenchinae.

Genera: *Aphelenchoides* Fischer, 1894 (syn. *Chitinaphelenchus* Micoletzky, 1922; syn. *Pathoaphelenchus* Cobb, 1927; sg. *Schistonchus* Cobb, 1927; sg. *Parasitaphelenchus* Fuchs, 1930); *Paraphelenchus* Micoletzky, 1922; *Tylenchulus* Cobb, 1913; *Nemonchus* Cobb, 1913; *Heterodera* Mueller, 1883 (syn. *Meloidogyne* Goledi, 1889; syn. *Heterobolbus* Raillet, 1896; syn. *Caconema* Cobb, 1894); *Aphelenchus* Bastian, 1865 (syn. *Isonchus* Cobb, 1913); *Rotylenchus* n. g. (type *T. robustus* de Man, 1880); *Pratylenchus* n. g. (type *T. pratensis* de Man, 1880); *Chitinotylenchus* Micoletzky, 1922; *Tylenchorhynchus* Cobb, 1913; *Tylenchus* Bastian, 1865; *Psilenchus* de Man, 1922; *Ditylenchus* n. g. (type *A. dipsaci* Kühn, 1859); *Anguillulina* Gervais et van Beneden, 1859; *Neotylenchus* Steiner, 1931; *Iotonchium* Cobb, 1920; *Hexatylus* Goodey, 1926; *?Macroposthonia* de Man, 1880; *Hemicycliophora* de Man, 1922; *Eutylenchus* Cobb, 1913; *Ecphyadophora* de Man, 1922c; *?Myenchus* Schuberg and Schroeder, 1904.

Subfamily Sphaerulariinae.

Genera: *Aphelenchulus* Cobb, 1920; *Tylenchinema* Goodey, 1930; *Allantonema* Leuckart, 1884; *Howardula* Cobb, 1921; *Parasitylenchus* Micoletzky, 1922; *Bradynema* Zur Strassen, 1892; *Atractonema* Leuckart, 1887 (syn. *Asconema* Leuckart, 1886, preocc.); *Sphaerularia* Dufour, 1837.

Subfamily Hoplolaiminae.

Genera: *Paratylenchus* Micoletzky, 1922; *Atylenchus* Cobb, 1913; *Procriconema* Micoletzky, 1925; *Hoplolaimus* Daday, 1905; *Criconema* Hofmänner and Menzel, 1914; *Iota* Cobb, 1913 (syn. *Ogma* Southern, 1914).

KEY TO SUBFAMILIES OF TYLENCHIDAE

1. (4) Mouth capsule prominent, wide or narrow, with or without teeth, always spearless.
2. (3) No special knoblike appendages of the mouth capsule. The form of the mouth capsule variable. **Diplogasterinae**
3. (2) The narrow mouth capsule has two knoblike hollow appendages .... **Tylopharynginae**
4. (1) Mouth capsule very narrow, spear-bearing, in some genera obsolete together with the spear.
5. (8) Spear with or without basal knobs, not very large and strong; lost in some genera.
6. (7) Free-living and plant parasitic. Body of typical nematodelike appearance in free-living forms, swollen in the females of some plant-parasitic species, but without large swollen cells inside. **Tylenchinae**
7. (6) Insect parasites. Body of typical appearance in young stages, swollen in mature parasitic females, in some genera losing the nematodelike body form; with swollen cells inside ....**Sphaerulariinae**
8. (5) Spear strong and huge, always cephalated. Cuticle with peculiar annulation .... **Hoplolaiminae**

The prominent feature of this family is the structure of the esophagus, muscular in the anterior part with a well-differentiated middle bulbus, and glandular in the posterior part. In most of the members of the Tylenchinae, as well as in the Diplogasterinae, the posterior portion of the esophagus is joined together and the boundary between it and the intestine is easily seen. In other Tylenchinae, e.g., *Aphelenchus,* the esophagus is subject to further evolution, the esophageal glands come out of direct connection with the body of the esophagus, the tubular portion becomes narrow, and its connection with the intestine cannot be easily observed; sometimes that part of the esophageal tube becomes short and the beginning of the intestine is quite near to the nerve-ring. In another direction there is a reduction of the anterior muscular part of the esophagus. Throughout there is a reduction in the functions of the esophagus. In most of the species of genera which contain plant-parasitic species, the only remaining muscular part is the middle bulb. A further reduction is to be seen in males of many other plant- or animal-parasitic or semiparasitic species in which the adult male does not feed; therefore this reduction is especially confined to males. The peak of the reduction comes in the Sphaerulariinae, parasites of the body cavity of insects. In that group the esophagus and the intestine do not function and the feeding is done through the skin. In some genera the esophagus is still retained, but is always rudimentary and functionless; in others, as in *Allantonema* and *Bradynema,* it is lost completely.

In the simpler genera of the Diplogasterinae there is an unarmed mouth capsule very similar to that of *Rhabditis*; in other genera it is armed with a tooth or teeth (fig. 64) different in different genera. The old genus *Diplogaster,* which, until now, united nearly all the species of the subfamily, must be resolved into several independent genera very distinctly characterized. Some types were given during the last few years by Rahm and Goodey, but the analysis seems to be not yet complete. The earthworm parasite, *Ungella,* apparently should be placed here; the hooklike onchia could be considered as homologous to the teeth of *Diplogaster,* and the preneural esophageal swelling is well developed, but there does not seem to be a sharp division between the two parts of the esophagus as in typical members of the Diplogasterinae.

Tylopharynx, the only genus of the next subfamily, was described by de Man as having three separate rods, united in Tylenchinae into a triple spear, a tylenchoid parallel to the tylencholaimoid *Diphtherophora.* The recent description given by Goodey (1929) gives a totally different interpretation of the structure of its mouth parts. There are not three, but only two knobs, hollow inside, chitinous ampullae of the esophageal glands. The position of the genus therefore becomes isolated.

The Tylenchinae are characterized by a triple spear very like that of *Tylencholaimus* but mostly with a strongly marked triple enlarged base (fig. 67).

Here must be located the previously mentioned body cavity parasites of the insects, the Sphaerulariinae. The more primitive forms like *Aphelenchulus, Howardula,* and others retain a well-developed spear; *Allantonema* has lost it, together with the esophagus. Although the different genera present some peculiarities in structure and in grade of parasitic reduction, they all have a very peculiar and similar life cycle. The larvae are liberated into the body cavity of the host, they grow inside the host, then leave its body through the anal or genital opening, and after a molt reach maturity outside the body of the host, in the soil, the burrows of wood-eating beetles, etc. The males reach full maturity, but the females have the ovary undeveloped and without direct connection with the uterus; the vulva is open. Then copulation takes place, the males die, and the fertilized female goes through the skin of a new host into the body, where it grows to the mature parasitic stage.

The Hoplolaiminae should be treated as a separate subfamily (fig. 68). The cuticle has peculiar rings, sometimes subdivided to give a scalelike appearance. There is a peculiar huge spear with proximal knobs. It is a highly specialized terrestrial group.

Family STRONGYLIDAE

The Strongylidae must be placed as a third family of this order. This large parasitic group was considered as a family long ago; now it is usually recognized as an order. The first-stage larvae are very distinctly similar to some free-living forms of the genus *Rhabditis.* The two dilatations of the esophagus, the posterior one with a masticatory apparatus, and the cylindroid mouth capsule are very similar to *Rhabditis.* The free life of strongylid larvae, and their molts with the ensheathed migratory third stage, correspond strictly to that described by Maupas in *Rhabditis.* Even in the adult stage, the characteristic bursa in typical cases, with its 20 rays, is comparable to that of some species of *Rhabditis* (cf. figs. 62, 63, and 70).

A systematic conclusion from these very real similarities could only be similar to that arrived at in analogous circumstances by the carcinologists in placing the aberrant Rhizocephala in the order Cirripedia, and, similarly, the parasitic copepods with the free-living forms in the Copepoda.

Order OXYURATA

The Oxyurata with their tripartite esophagus and masticatory cardiac bulb could be compared with the free-living Anguillulata. It is even difficult to find clear diagnostic characters to separate these two orders. Steiner (1923) described a parasite from a sawfly larva and because of its general similarity he referred it to the oxyurid genus *Aplectana* with all its other species intestinal parasites of Amphibia and Reptilia. (Now it is referred to a separate genus, *Steinernema.*) The writer found a very closely related species, probably congeneric with Steiner's, in a cutworm, fortunately accompanied by their larvae which proved to be typically rhabditoid; the influence of parasitism can also give very similar results in both orders, which is an indirect evidence of their affinity. The chief difference seems to be their biology: the Oxyurata are parasites from the first stage to the last—no free-living larvae seem to exist among them; there is no clear metamorphosis in this group. A larva just hatched is always readily recognized as a young oxyurid, generally very similar to the adult stage except for its size and genital organs. It could be said that the Oxyurata are modified by parasitism from the beginning to the end of their lives, contrary to which the parasitic Anguillulata always conserve some free-living stage and their larvae are similar to the free-living forms of the order.

Another distinction could be found in the physiology of both orders. As was said, the general character of the free-living Anguillulata is their impermeable thick cuticle; it is fully conserved and even strengthened in the not numerous intestinal parasites belonging to the order, such as *Cephalobium*. The musculature is strong and the movement quick and alert, the body cavity is generally filled up by different cells and conserved only as fine clefts between them. Quite otherwise is the general constitution of the Oxyurata. The cuticle is fine, impermeable enough for organic bodies, but not for water, which easily passes through it. The body cavity is well developed and filled with a fluid content. The body is swollen and its walls are stretched from the inside by the turgor thus arising; it can be easily proved by damaging the body walls, the body cavity fluid, together with the inner organs, being then ejected with force. The semipermeability of the cuticle can easily be demonstrated by placing these nematodes in solutions of different osmotic strengths. The solutions with higher osmotic pressure will produce a general squeezing of the body and finally even the separation of the cuticle and hypodermis, and the further squeezing of the body inside the cuticle, the general picture being then very like that of plasmolyzed plant cells. The solutions with higher osmotic pressure will produce a general swelling and tension of the body and sometimes even its bursting. The musculature of most of the Oxyurata is meromyarian and platymyarian, therefore very weak, and the movements are slow and clumsy.

This order seems to be very natural. The writer does not understand very well why it was separated in several independent families by Baylis and Daubney (1926), but probably it was on purely taxonomic grounds; the elimination of several genera into the Rhabdiasata (i.e., Anguillulata in our classification) by Travassos (1930) seems also to be inadequate. The more common way of uniting them into one order, as was originally proposed by Railliet and

Henry (1915), then followed by Skrjabin (1923), Yorke and Maplestone (1926), and others, seems to be much happier.

The vertebrate parasites in general have been soundly placed in the system of classification, but the same hardly could be said about the parasites of arthropods monographed in recent years in Brazil (Travassos, 1929; Artigas, 1930). In these papers the Brazilian authors tried to build up a system quite independent from the existing system of parasites of vertebrates. But the parasites of invertebrates cannot be considered as different from other Oxyurata as a whole. The one-spiculed genera of oxyurids of arthropods are so similar to the one-spiculed genera of oxyurids of vertebrates that they can not be separated and must be referred to the same systematic group. Travassos (1930) himself in a later paper came to the same general conclusions in trying to build a system embracing both biological groups. Several hints from his work are used in the sketch of the system below.

In the review below there is given the systematic distribution of oxyuroid genera parasitic in invertebrates only. For the parasites of vertebrates Yorke and Maplestone (1926) and Baylis and Daubney (1926) should be consulted.

KEY TO FAMILIES OF OXYURATA PARASITIC IN INVERTEBRATES

1. (6) Spicules two (obsolete in some Kathlaniidae).
2. (3) Male without a preanal sucker .... **Atractidae**
3. (2) Male with preanal sucker or pseudosucker developed as a differentiation of precloacal musculature.
4. (5) Polymyarian. Lips poorly developed .... **Heterakidae**
5. (4) Meromyarian. Lips strongly developed, well separated .... **Kathlaniidae**
6. (1) Spicule single .... **Oxyuridae**

SUBFAMILIES AND GENERA OF THE FAMILY ATRACTIDAE

Subfamily Cosmocercinae (including Oxysomatiinae).

Subfamily Atractinae.

Subfamily Carnoyinae, subfam. nov.

Genera: *Rondonema* Artigas, 1926; *Carnoya* Gilson, 1898; *Pararhabditis* Baylis and Daubney, 1926 (=*Pseudorhabditis* Szüts, 1912).

Subfamily Rhigoneminae Artigas.

Genera: *Dudekemia* Artigas, 1930; *Rhigonema* Cobb, 1898; *Ichthyocephalus* Artigas, 1926.

KEY TO SUBFAMILIES OF ATRACTIDAE

1. (6) Esophagus with its parts of very different diameters.

2\. (5) Esophagus long, with the middle part of uniform or nearly uniform diameter.
3\. (4) Female genitalia double .... **Cosmocercinae**
4\. (3) Female genitalia single, extending anteriorly ....**Atractinae**
5\. (2) Esophagus short, with the middle part forming an elongated ovaloid bulbus. Females with spines ..**Carnoyinae**
6\. (1) Esophagus with its three parts of nearly uniform diameter, thick and short .... **Rhigoneminae**

The subfamily Cosmocercinae (=Cosmocercidae Travassos, 1930) is here understood in the same way as was the corresponding family by Travassos, separating it thus from the one-spiculed forms. The Atractinae (=Atractidae Travassos) are separated from the Cosmocercinae because of the single female genitalia, but the males are so similar in both groups, and the separating character so secondary in most other families of Nematoda, that I have no doubt that both groups should be classified more closely than is done by most authors. Two groups from invertebrates must be added to them, (1) the Carnoyinae, highly specialized forms from Myriapoda and Oligochaeta, with a peculiar development of the esophagus and with sexual dimorphism, the females with spines in the anterior part of the body, and (2) the Rhigoneminae which have a short thick esophagus with all its three parts of nearly the same diameter.

Subfamilies and Genera of the Family Heterakidae

Subfamily Subulurinae.
Subfamily Heterakinae.

KEY TO SUBFAMILIES OF HETERAKIDAE

1\. (2) In males the precloacal sucker or pseudosucker without a chitinous rim .... **Subulurinae**
2\. (1) In males the precloacal sucker well defined with a chitinous rim .... **Heterakinae**

The outlines of the family and both subfamilies are accepted as by Baylis and Daubney (1926). Both subfamilies are united by some transitions. The suckers of the second subfamily are undoubtedly a development of the pseudosuckers of the first one. Travassos (1930) proposed to separate the Spinicaudinae, a proposal which undoubtedly has some grounds. The genera included here are polymyarian and have feebly developed lips, a character which separates them from the following family.

Subfamilies and Genera of the Family Kathlaniidae

Subfamily Kathlaniinae.
Genera: *Oniscicola* Schwenck, 1927; *Cruznema* Artigas, 1926.

Subfamily Cissophyllinae.
Subfamily Cruziinae.
Subfamily Ransomneminae Travassos.
  Genera: *Ransomnema* Artigas, 1926; *Heth* Cobb, 1898 (syn. *Streptogaster* Cobb, 1898); *Clementeia* Artigas, 1930.
Subfamily Lepidoneminae Travassos.
  Genera: *Lepidonema* Cobb, 1898; *Hystrignathus* Leidy, 1850 (syn. *Xyo* Cobb, 1898); *Pulchrocephala* Travassos, 1925.

KEY TO SUBFAMILIES OF KATHLANIIDAE

1. (8) Spicules present.
2. (7) Esophagus long, typically developed.
3. (6) Intestinal caecum absent.
4. (5) Lips without teeth and lamellae .... **Kathlaniinae**
5. (4) Lips armed with powerful teeth and lamellae ...**Cissophyllinae**
6. (3) Intestinal caecum present .... **Cruziinae**
7. (2) Esophagus with swollen medial part .... **Ransomneminae**
8. (1) Spicules absent, some chitinous parts (?gubernaculum) present but not evaginable; copulation by apposition of genital openings .... **Lepidoneminae**

The Kathlaniidae include all genera with a sucker in the male and with meromyarian musculature, our definition thus coming very near to that of Baylis and Daubney (1926), and including the Cruziidae separated by Travassos. The chief ground for separation of the last is the presence of the intestinal caecum in *Cruzia,* but it is safer to take the taxonomic characters from the more constant mouth parts and male genitalia than from the parts of intestine which are variable in very closely related groups. The Cissophyllinae as separated by Yorke and Maplestone (1926) are based on their specialized mouth parts. Three groups from the invertebrates can be included here. *Oniscicola* and *Cruznema,* with a typical development of the esophagus, can be included directly in the Kathlaniinae. The Ransomneminae should be separated because of the peculiar development of the esophagus which is swollen in its medial part. The Lepidoneminae which have lost the spicules are very peculiar, but also can be classed here because of the preanal sucker which is developed or at least rudimentary.

SUBFAMILIES AND GENERA OF THE FAMILY OXYURIDAE

Subfamily Oxyurinae.
  Genera: *Thelastoma* Leidy, 1854 (sg. *Thelastomellum* Cobb, 1929; syn. *Bulhõesia* Schwenck, 1926); *Leidynema* Schwenck, 1929; *Severianoia* Schwenck, 1926; *Cephalobellus* Cobb, 1920 (syn. *Blatticola* Schwenck, 1926); *Binema* Travassos, 1925; *Protrellus* Cobb, 1920; *Pseudonymus* Diesing, 1857 (syn. *Ptychocephalus* Diesing, 1861; syn. *Helicothrix*

Galeb, 1878); *Aorurus* Leidy, 1854 (syn. *Streptostoma* Leidy, 1854; syn. *Blattophila* Cobb, 1920).

Subfamily Syphaciinae.

Genus: *Angra* Travassos, 1929.

KEY TO SUBFAMILIES OF THE OXYURIDAE

1. (2) Males without a gubernaculum .... **Oxyurinae**
2. (1) Males with a gubernaculum .... **Syphaciinae**

Here are united most of the known one-spiculed forms of the Oxyurata, with numerous genera and species in both Vertebrata and Invertebrata. The idea of separating them from other Oxyurata belongs to Travassos (1930). The further division as proposed by Walton (1929) and Travassos (1930) would be difficult to follow without a more complete consideration of the subject. The old division proposed by Raillet and Henry (1916) and followed by Yorke and Maplestone (1916) should therefore be accepted at this time.

Orders ASCARIDATA, SPIRURATA, FILARIATA, DIOCTOPHYMATA and TRICHURATA

Parasitism always transforms an animal. The free-living stages of the Strongylidae saved for us the evidence of their true nature; it is probable that because of the semisaprozoic life of the Oxyurata they conserved traces of typical resemblance to the Anguillulata. But the other parasitic orders do not possess free-living stages and are more specialized in their parasitic life.[4] Thus little could be said about their relationships.

The comparatively small and highly specialized groups of Dioctophymata and Trichurata could be considered as very isolated and natural. The relations between the other orders seem to be not as yet worked out. The Spirurata will probably be subject to most modifications. But the wisest course for the moment would be to keep all the three separate as Yorke and Maplestone have done.

Wülker (1929) has recently suggested a direct relation between the Ascaridata from marine fishes and some free-living groups, thus assuming an evolution of this order independent from other parasitic orders. But it is highly probable that the Ascaridata have had a different mode of evolution, probably a much longer one and one bound with some other parasitic groups.

CONCLUSION

In the writer's opinion the classification of today, especially that of the lower groups, is in reality the same as it was in the time of

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[4] An exception are the free-living larvae of *Camallanus,* but these have never been studied in detail.

Linné, i.e., the registration of similarities and dissimilarities, only a little and superficially colored by the theory of evolution. The similarities alone have a value for the building of a natural system. The absence of some distinct feature or the presence of one, should not be a cause of the exclusion of some form from a group when other characters are similar. No character is important by itself, but only in its more or less wide occurrence among similar forms. For this reason I do not hesitate to range a spiral-amphid *Tripyloides* among other pocket-amphid Enoplata, and because of these principles it seems to me wise to class the Strongylidae within the Anguillulata.

Each systematic arrangement of a group, with very rare exceptions, passes, it seems, through three stages. The first is that of chaos, the second is the putting of the closely similar side by side, and the third is a definite classification upon the basis of real resemblances. Stiles and Hassall (1926) are, of course, right in saying that a natural system of the Nematoda is in the stage of making; it seems that we are gradually passing through the second stage, and are rather in it than in the first one.

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EXPLANATION OF PLATES

Order ENOPLATA

PL. 1, FIG. 1. *Mononchus trichurus* Cobb, the female showing some typical characters of the order. Note the smooth cuticle, the plain bulbless esophagus, and the female genitalia with the reflected ovaries. *a,* top of ovary; *b,* base of ovary; *c,* oviduct; *d, e,* top part of uterus transformed into a receptaculum seminis with sperm inside; *f,* egg in the main part of the uterus; *g,* genital opening; in typical cases there are two ovaries. After Cobb, 1917.

FIG. 2. *Leptosomatum bacillatum* (Eberth) showing the typical head structure of the Enoplidae. Note the wide surface by which the esophagus attaches to the cuticle anteriorly, the duplication of the cuticle with the "circumoral pocket" between the two layers, and the pocketlike amphid. After Filipjev, 1918.

FIG. 3. *Thoracostoma coecum* Saveljev, showing an example of a highly developed cephalic capsule. After Filipjev, 1927.

FIG. 4. *Enoplus communis* Bastian, showing the head viewed from the side and a little ventrally. Note the three typical jaws, surrounded by the ring of the cephalic capsule, the amphids, and the cephalic organ anterior to them, the cephalic line. After de Man, 1886.

FIG. 5. *Enoplus communis* Bastian, showing the head viewed *en face.* Note the typical disposition of the 10 cephalic setae and 6 labial papillae; note also the symmetrical disposition of the 3 jaws. After de Man, 1886.

FIG. 6. *Enoploides amphioxi* Filipjev, a head showing the jaws split behind, the lips highly developed, and the setiform labial papillae. After Filipjev, 1918.

FIG. 7. *Enoplolaimus lucifer* Filipjev, showing the head with the jaws transformed in a framework of the mouth capsule, and an onchium between the two posterior prolongations. Note the cephalic organ pointing externally. After Filipjev, 1927.

FIG. 8. *Oxystomina elongata* (Bütschli), showing the elongated head, the four sublateral setae shifted backwards to form a second circle, and the amphid very far behind and with an enlarged orifice. After de Man, 1907.

FIG. 9. *Halalaimus diplocephalus* Filipjev, showing the amphids elongated to form a longitudinal slit. After Filipjev, 1927.

FIG. 10. *Phanoderma conicaudatum* (Steiner). Note the four-lobed cephalic capsule, the eye with a well-defined lens, and the far-advanced cervical pore. After Filipjev, 1927.

FIG. 11. *Oncholaimus conicauda* Filipjev, showing a typical mouth capsule with three onchi and the "circumoral pocket". After Filipjev, 1929.

FIG. 12. *Rhabdodemania major* (Southern). Note that the mouth capsule with three onchi is comparable to that of the On-

cholaiminae, but the lips are more complicated. After Southern, 1913.

FIG. 13. *Eurystomina assimilis* (de Man), showing the mouth capsule without lips; the large onchium can be protruded outside the capsule. After Filipjev, 1918.

FIG. 14. *Eurystomina assimilis* (de Man), showing the male tail. Note the strongly curved, thin spicules and the two preanal organs. After Filipjev, 1918.

PL. 2, FIG. 15. *Symplocostoma ponticum* Filipjev, showing a mouth capsule very similar to that of *Eurystomina;* in addition to the chief onchium or spear, there is a little guiding onchium on its side; a part of the bottom of the mouth capsule has become isolated, forming the cuticular "lens." After Filipjev, 1918.

FIG. 16. *Enchelidium longicolle* Filipjev, supposed to be the male of a symplocostomoid female; the mouth capsule is reduced except for the "lenses". After Filipjev, 1918.

FIG. 17. *Trilobus brevisetosus* (W. Schneider), showing the large mouth capsule followed by a back chamber with two little denticles inside; there is no "circumoral pocket". After Filipjev, 1929.

FIG. 18. *Tripyloides marinus* (Bütschli). Note that the general shape of the mouth capsule recalls that of *Trilobus,* but the mouth can be opened wide as in *Tripyla;* the amphids are spiral. After Filipjev, 1929.

FIG. 19. *Halanonchus macrurus* Cobb. Note that this is similar to other Tripyloidinae as regards its spicular apparatus, but it has a pocketlike amphid. After Cobb, 1920.

FIG. 20. *Dorylaimus regius* de Man, showing its typical "dorylaimoid" esophagus, narrow anteriorly and gradually widening posteriorly. After Steiner, 1927.

FIG. 21. *Tylencholaimus mirabilis* (Bütschli), showing the head with the three-lobed spear. After de Man, 1884.

FIG. 22. *Hygolaimus menzeli* Micoletzky, with the spear distinctly on one side of the mouth capsule. After Micoletzky, 1925.

FIG. 23. *Dorylaimus stagnalis* Dujardin, with the typical spear guided by the two vestibular rings. After Filipjev, 1929.

FIG. 24. *Dorylaimus regius* de Man, showing the tail of the male. Note the wide spicules with a longitudinal chitinous ridge in the middle, the preanal median row of papillae, and the strong bursal musculature. After Steiner, 1927.

FIG. 25. *Mermis nigrescens* Dujardin, showing the tail of the male. Note that the strong bursal musculature and the preanal row of papillae recall the Dorylaimidae. After Hagmeier, 1913.

FIG. 26. *Mermis tenuis* Hagmeier, showing the head with the huge pocketlike amphids. After Hagmeier, 1912.

Order CHROMADORATA

FIG. 27. *Paraplectus pedunculatus* (Hofmänner). Note the striated cuticle, the long and narrow mouth capsule, the strongly marked amphid, and the thickening of the cuticle anteriorly. After Filipjev, 1929.

FIG. 28. *Dermatolaimus steineri* Filipjev. Note the anterior thickening of the cuticle, more or less wide attachment of the esophagus to it, and the amphid, which is round with a posterior prolongation. After Filipjev, 1922.

FIG. 29. *Aphanolaimus attentus* de Man. Note the peculiar amphids. After de Man, 1884.

FIG. 30. *Aphanolaimus attentus* de Man, side view. After de Man, 1884.

FIG. 31. *Cyatholaimus demani* Filipjev, showing the *en face* view of the head. Note the 12-fold vestibulum and the dorsal onchium in the mouth capsule. After de Man, 1889b.

FIG. 32. *Cyatholaimus demani* Filipjev, side view. Note the 6 labial papillae, 10 cephalic setae, the folds of the vestibulum, the onchium, the spiral amphid, the points of the cuticle, and the eye, and compare with the preceding figure. After de Man, 1889b.

PL. 3, FIG. 33. *Halichoanolaimus filicauda* Filipjev, lateral view of the head. Note the two chambers of the mouth capsule, and the amphids and cuticle like those of *Cyatholaimus*. After Filipjev, 1918.

FIG. 34. *Halichoanolaimus filicauda* Filipjev, view *en face*. Note the true lips with the labial papillae. After Filipjev, 1918.

FIG. 35. *Halichoanolaimus filicauda* Filipjev, showing at a deeper focus the 12 rods of the anterior part of the mouth capsule, the 3 spines and the comblike apparatus marking the boundary of its two parts. After Filipjev, 1918.

FIG. 36. *Cheironchus bulbosus* (Filipjev). Note the two high lips, with huge labial papillae, the spiral amphids, and the two powerful jaws. After Filipjev, 1918.

FIG. 37. *Cheironchus bulbosus* (Filipjev), ventral view. After Filipjev, 1918.

FIG. 38. *Cheironchus bulbosus* (Filipjev), view *en face*. Note the two jaws, the dorsal rudimentary lip, and the disposition of the papillae and cephalic setae. After Filipjev, 1918.

FIG. 39. *Synonchium obtusum* Cobb, a nematode with three jaws like *Enoplus*. The cuticle and amphids are like those in the Cyatholaiminae and the other genera of the Choanolaiminae. After Cobb, 1920.

FIG. 40. *Synonchium obtusum* Cobb, showing the mouth open and the lips protruded. After Cobb, 1920.

PL. 4, FIG. 41. *Richtersia collaria* Steiner. Note the characteristic short and thick body form, and the longitudinal striation produced by rows of minute cuticular spines; the powerful esophagus, spiral amphids and pointed cuticle leads to a comparison with the Cyatholaiminae. After Steiner, 1916.

FIG. 42. *Odontonema guido-schneideri* Filipjev, a representative of the Chromadorinae, with a little spiral amphid placed far forward; the large tooth of the mouth capsule is characteristic for a few genera. Note the anterior cephalic circle represented by papillae. After Filipjev, 1929.

FIG. 43. *Prochromadorella viridis* (Linstow), with the amphid spiral flattened to form a transverse slit; this genus and some other genera of the Chromadorinae have three teeth in the buccal capsule. After Filipjev, 1929.

FIG. 44. *Metachromadora macroutera* Filipjev; the plain strong rings of the cuticle are characteristic of all the Desmodorinae, but the peculiar striation of the head only for a few of them. After Filipjev, 1918.

FIG. 45. *Monoposthia mielcki* Steiner; the plain rings of the Monoposthiinae are interrupted by rows of longitudinal crests or spines; a desmodoroid parallel to *Richtersia;* note the roundish amphid. After Steiner, 1916.

FIG. 46. *Ceramonema annulata* (Filipjev); the four longitudinal crests of the cuticle are like those of the Monoposthiinae; the much-reduced mouth structure and the horseshoe-shaped amphid resemble those of the Draconematinae; the huge rings of the cuticle are very distinctive. After Filipjev, 1922.

FIG. 47. *Epsilonema (?) cygnoides* (Metchnikov). Note the peculiar form of the body with its "neck" and the adhesive nontubular setae in the middle part of the body. After Steiner, 1916.

PL. 5, FIG. 48. *Draconema cephalatum* Cobb, a marine nematode of worldwide distribution. There is not only a "neck," but also a "head"; the adhesive setae are tubular (one under a higher magnification is shown right below), and are disposed in two groups, on the head and in several preanal rows (four in that genus). After Cobb, 1913.

Order DESMOSCOLECTATA

FIG. 49. *Desmoscolex minutus* Claparède. The huge secreted cuticular rings are very prominent; the disposition of the ambulatory setae is peculiar to each species. After Filipjev, 1922.

FIG. 50. *Quadricoma reinhardi* Filipjev, a species with 43 secreted rings. After Filipjev, 1922.

Order MONHYSTERATA

FIG. 51. *Theristus sentiens* (Cobb), a general view of the female to show the female genitalia with the straight ovaries characteristic of the order. *a,* the ovarial part of the gonad; *b,* the oviduct part (*a* and *b* are fused together); *c,* uterus with an egg inside; *d,* vaginal opening; *e,* the rudiment of the posterior gonad. After Cobb, 1914.

PL. 6, FIG. 52. *Theristus setosus* (Bütschli). One can see the large vestibulum, the chitinous ring supporting the esophagus, and the spiral amphids. Note the supporting rods of the vestibulum. After Filipjev, 1929.

FIG. 53. *Sphaerolaimus hirsutus* Bastian. The chitinous ring of the mouth capsule becomes very large, giving place to a spacious mouth capsule inside; the rods in the walls of the vestibulum are better developed. Afer de Man, 1907.

FIG. 54. *Comesoma stenocephalum* Filipjev. Note the huge spiral amphid, the six labial and six cephalic papillae, and the four cephalic setae, followed by subcephalic ones. After Filipjev, 1918.

FIG. 55. *Linhomoeus lepturus* de Man. Note the thin cuticle, the feebly developed chitinous ring of the mouth capsule, and the round, thick-walled amphid, or what might be called a spiral one in one turn. After de Man, 1907.

FIG. 56. *Linhomoeus lepturus* de Man, showing the spicules strongly curved and with a double backward-pointing gubernaculum; this is characteristic of all the members of the family Linhomoeidae. After de Man, 1907.

FIG. 57. *Dorylaimopsis perfectus* (Cobb), showing the double spicules; the gubernaculum is typical. After Cobb, 1920.

FIG. 58. *Dorylaimopsis perfectus* (Cobb), showing a side view. After Cobb, 1920.

FIG. 59. *Axonolaimus setosus* Filipjev, showing the head. The vestibulum and the mouth capsule are strongly developed; both branches of the horseshoe-shaped amphid are closely pressed together. After Filipjev, 1918.

FIG. 60. *Diplopeltis cirrhatus* (Eberth), showing the horseshoe-shaped amphid surrounded by a strongly chitinized plate. After Filipjev, 1918.

Order ANGUILLULATA

PL. 7, FIG. 61. *Rhabditis elegans* Maupas. Note the elongate mouth capsule, the preneural esophageal swelling, and the true cardiac bulb with the masticatory apparatus. After Maupas, 1900.

FIG. 62. *Rhabditis elegans* Maupas, showing the spicules and bursa in ventral view. After Maupas, 1900.

FIG. 63. *Rhabditis elegans* Maupas, a side view. After Maupas, 1900.

FIG. 64. *Diplogaster fictor* Bastian, showing a dorsal view of the head. Note the folds of the lips, the teeth of the mouth capsule, and the amphids. After Cobb, 1914.

FIG. 65. *Diplogaster fictor* Bastian, showing the esophagus separated into two parts with the preneural and cardiac bulbs. After Cobb, 1914.

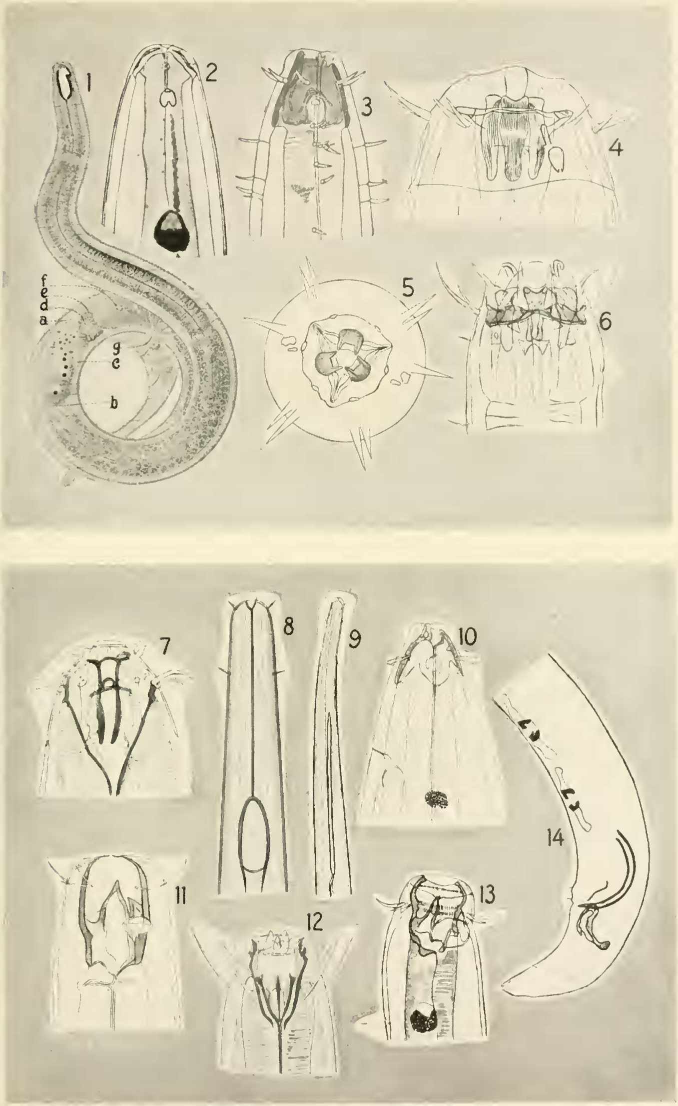
FIG. 66. *Bunonema ditlevseni* Micoletzky. The mouth capsule and the esophagus are distinctly rhabditoid, the asymmetrical cuticular knobs and head appendages are very distinctive. After Micoletzky, 1925.

PL. 8, FIG. 67. *Paratylenchus nanus* Cobb, a representative of a highly specialized genus of the Tylenchidae; the triple spear is very large, the preneural bulb is the only one that retains its musculature, the cardiac bulb being composed of gland cells only. After Cobb, 1925.

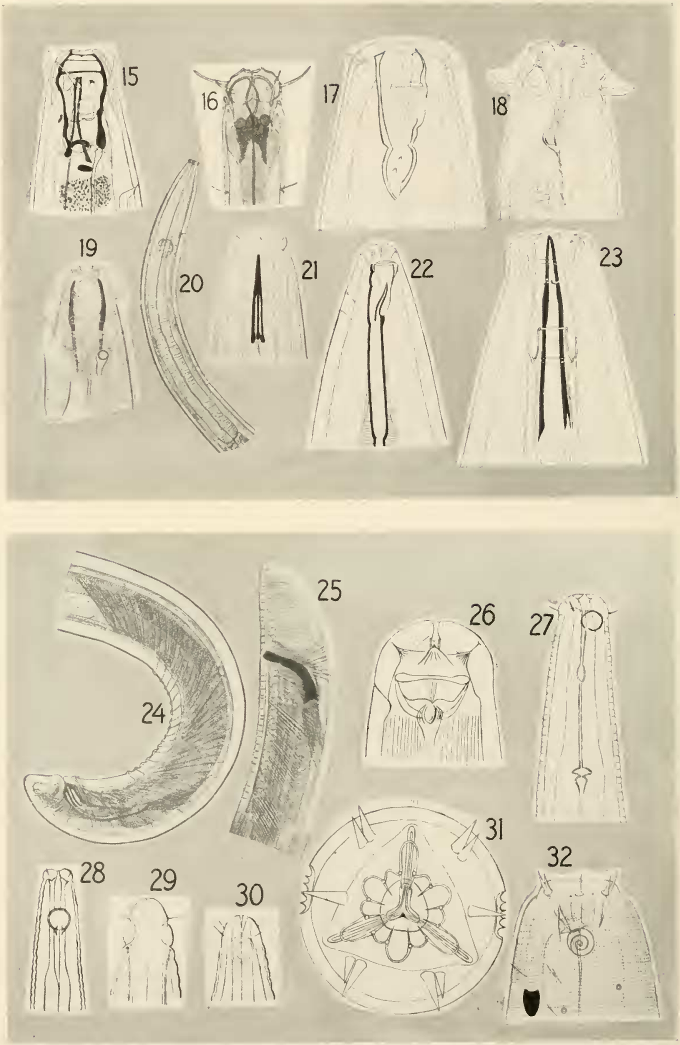
FIG. 68. *Iota octangulare* Cobb, another highly specialized form of the same family. Note the huge spear and the scalelike differentiation of the cuticle. After Cobb, 1914.

FIG. 69. *Rhabdias sphaerocephala* Goodey. Note the remnants of the preneural bulb, characteristic of the Anguillulata; in other species of the genus there are no more hints of it in the syngonic generation, but it is always very clear in the bisexual one. After Goodey, 1924.

FIG. 70. *Cylichnostomum auriculatum* Looss, showing the bursa of the male, characteristic of the males of all the members of the family Strongylidae to which it belongs; it could be explained as a specialization of the bursa of some form of Rhabditis (compare figs. 62 and 63). After Looss, 1901.

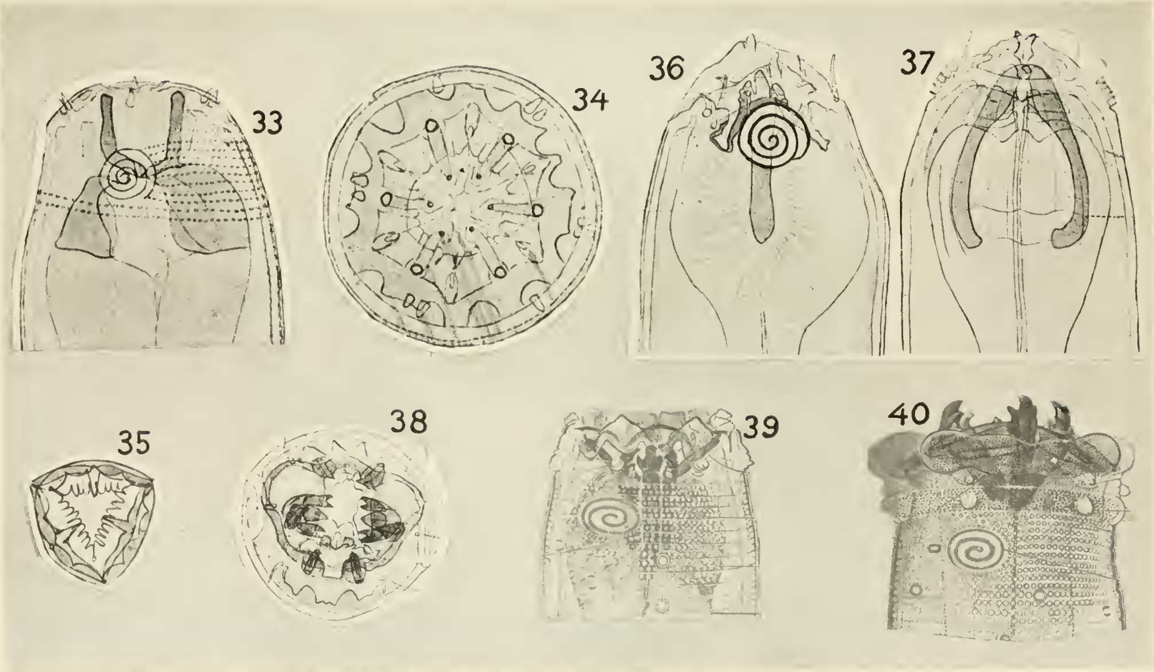


FREE-LIVING NEMATODES
(For explanation, see pages 58, 59)



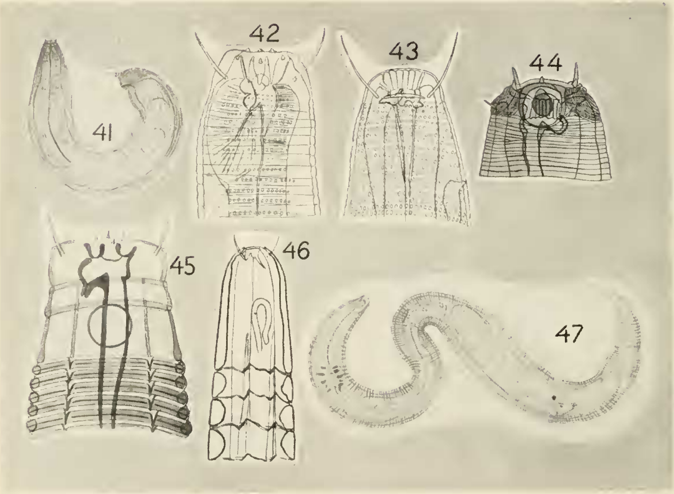
Free-Living Nematodes

(For explanation, see pages 59, 60)

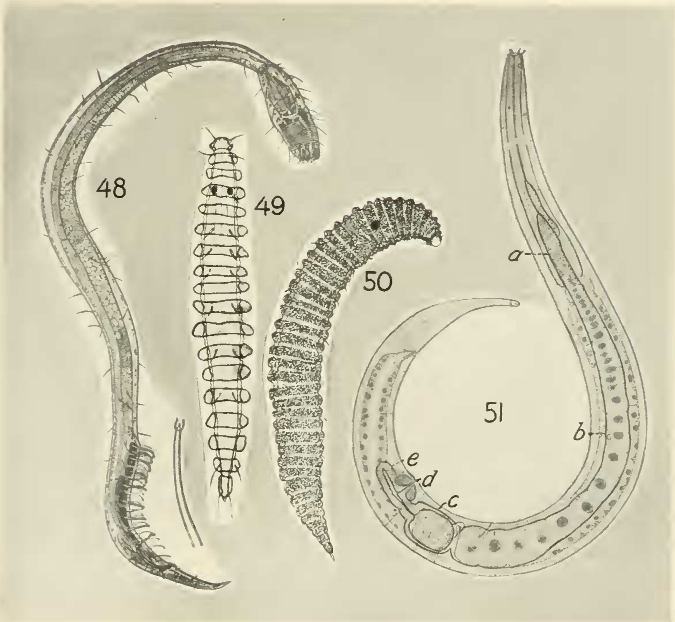


Free-Living Nematodes

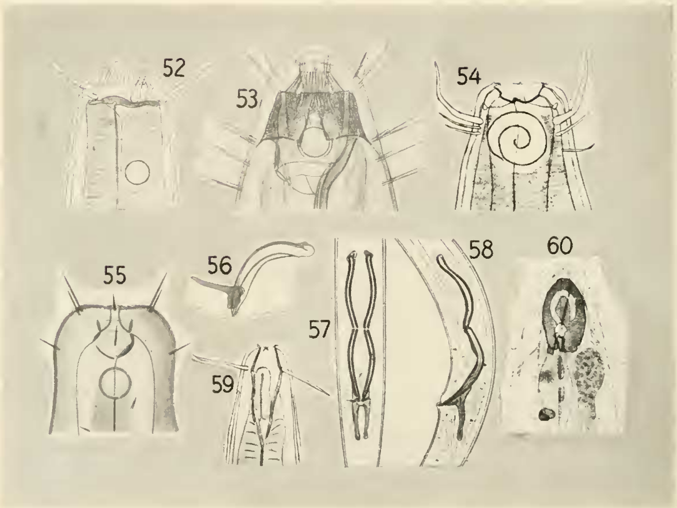
(For explanation, see page 60)



FREE-LIVING NEMATODES
(For explanation, see pages 60, 61)



FREE-LIVING NEMATODES
(For explanation, see page 61)



Free-Living Nematodes
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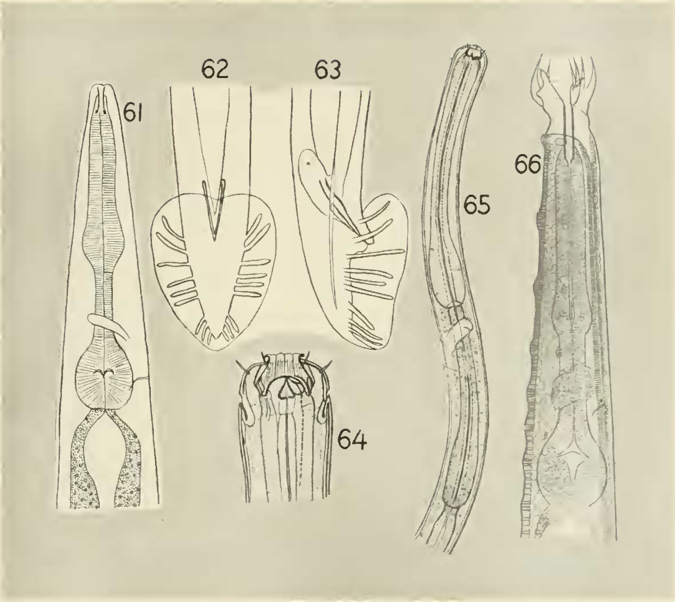
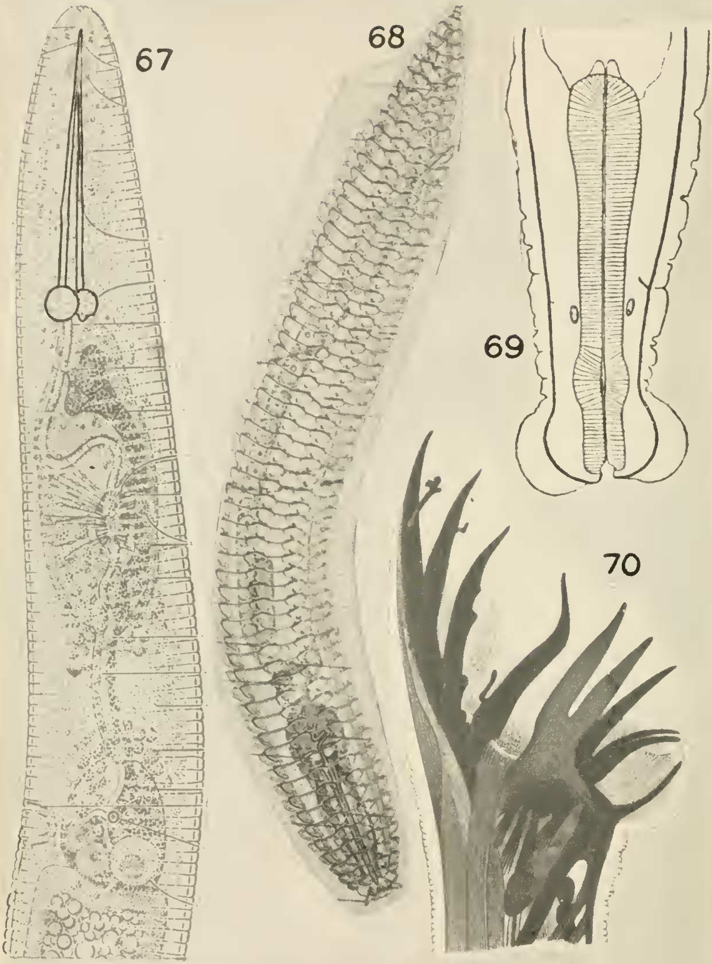


FREE-LIVING NEMATODES
(For explanation, see page 62)



Free-Living Nematodes
(For explanation, see page 63)